Fall 1977

A MONOGRAPHIC STUDY OF THE NEW ENGLAND CORYPHELLIDAE (GASTROPODA: OPISTHOBRANCHIA)

ALAN MITCHELL KUZIRIAN

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Keywords
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UNIVERSITY OF NEW HAMPSHIRE, PH.D., 1977

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A MONOGRAPHIC STUDY OF THE NEW ENGLAND
CORYPHELLIDAE (GASTROPoda: OPISTHOBRANCHIA)

by

ALAN MITCHELL KUZIRIAN
B.A., Northeastern University, 1969
M.S., Northeastern University, 1973

A THESIS

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This thesis has been examined and approved.

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ABSTRACT

A MONOGRAPHIC STUDY OF THE NEW ENGLAND
CORYPELLIDAE (GASTROPODA: OPISTHOBRANCHIA)

by

ALAN MITCHELL KUZIRIAN

The morphology, including reproductive anatomy, and
general ecology of Coryphella nobilis Verrill 1880, collected off the New England coast are discussed. Its egg mass
is described. Its annual life cycle includes development
to a planktotrophic veliger in 10 to 14 days. The predator-
prey relationship is discussed in relationship to several
proposed models. The taxonomic status of this species is
reviewed.

The external morphology, reproductive anatomy and
general biology of a new coryphellid nudibranch are given.
Its taxonomic position is discussed in relation to the
rare and little known species of Coryphella reported from
arctic regions of the Eastern and Western Hemispheres. A
new name, Coryphella zinfandella, is given to the specimens
Bergh (1886) misidentified as Gonieolis typica M. Sars 1861
while the genus Chlamylla Bergh 1886 is proposed as a
junior synonym of the genus Coryphella Gray 1850. The
validity of the genus Paracoryphella Miller 1971 is also
discussed.

The taxonomy and description of four coryphellid nudibranchs (Coryphella gracilis, C. pellucida, C. salmonacea, and C. verrucosa) found within the Gulf of Maine is presented. Their distribution, seasonality and prey preferences within this area are discussed relative to the European data. The ecology and coexistence of these and two other coryphellid species are discussed in terms of their dominance of the New England nudibranch fauna.
GENERAL INTRODUCTION

Literature available on the Nudibranchia from the middle and closing years of the last century is mostly taxonomic. Scattered throughout these reports are morphological descriptions and diagrams of many new species. The epitome of this taxonomic and descriptive era was reached in Alder & Hancock's (1845-55) monograph on the British Nudibranchiate Mollusca. At the end of the last century, and into this quarter century, the emphasis turned toward histological investigations of nudibranch organ systems as seen in the writings of Hecht, Pelseneer, Henneguy and Trinchese. Since Chambers (1934), the literature has contained more information relating the various anatomical structures to their functional morphology and to the animal's biology. During this entire period, over twenty species of Coryphella were described. The taxonomic status and validity of many of these species were changed regularly by various authors and even today the validity of several species remains unknown.

Although Odhner (1939) has classified the genus Coryphella as the most primitive of the aeolid nudibranchs, the congeners demonstrate a natural evolutionary line of advancement and successive specialization. Evidence to support this statement can be found when their external morphology and the anatomy and functional morphology of their reproductive systems are analyzed (Kuzirian, 1973).
The more primitive coryphellids possess a large, broad and somewhat flattened body form, numerous evenly distributed cerata and a structurally primitive reproductive system. The most advanced congeners are narrower, taller in body height, possess reduced numbers of cerata arranged in specific clusters, and have morphologically advanced reproductive systems. Among the New England coryphellids, there are two primitive species, two advanced species, and two species demonstrating characteristics intermediate between both groups. Such a high diversity of coryphellid nudibranchs in such a narrowly defined geographic area is only equalled by the high diversity found over the much larger expanse of the northern European coasts.

Since Odhner's (1939) publication there has not been a comprehensive review of the European coryphellids, although Thompson & Brown (1976) have recently reviewed those found in the British Isles. Except for Gould & Binney's (1870) summary of the older works on new species descriptions, the meager accounts of occurrences and distributional data by Balch (1908, 1909), Johnson (1915, 1934), and Verrill (1879, 1880, 1882) and the more recent partial reviews by Moore (1964) and Meyer (1971), there has never been a complete review of the New England coryphellids. The taxonomy of this genus is still very confused both for the New England and European species. The internal anatomy of several New England species has not been described and one recently discovered species has yet to be described.
and named. The biological data of all the New England species is still very incomplete. For these reasons, I have undertaken a monographic review of the New England Coryphellidae. The first chapter deals with the taxonomy, description and biology of Coryphella nobilis Verrill 1880. This species had not been confirmed in New England since Verrill's original findings and the discovery of a substantial population of C. nobilis off the New Hampshire coast has allowed a study of its biology. Chapter two contains the description and biology of a new species Coryphella verrilli as well as a comprehensive review of the genus Chlamylla Bergh 1886, and Paracoryphella Miller 1971. The third chapter contains the taxonomy, geographic distributions, descriptions and biology of the four remaining New England coryphellids: C. gracilis, C. pellucida, C. salmonacea and C. verrucosa. It is hoped that this review will provide a definitive resolution to the taxonomy of this genus in New England and that the biological problems left unresolved will stimulate further research.

**Literature Cited**


CHAPTER I

REDISCOVERY AND BIOLOGY OF CORYPHELLA NOBILIS
VERRILL 1880, IN NEW ENGLAND
(GASTROPODA: OPISTHOBRANCHIA)

Abstract

The morphology, including reproductive anatomy, and general ecology of Coryphella nobilis Verrill 1880, collected off the New England coast are discussed. Its egg mass is described. Its annual life cycle includes development to a planktrophic veliger in 10 to 14 days. The predator-prey relationship is discussed in relationship to several proposed models. The taxonomic status of this species is reviewed.

Introduction

Coryphella nobilis Verrill 1880, was described from a single specimen dredged off Cape Cod. Later Verrill (1882), figured the radula. Since these initial publications, Coryphella nobilis has only appeared in the New England literature as a listing among the New England nudibranch fauna (Johnson, 1915, 1934; Franz, 1970). From the European literature, little more than distribution, depth, and bottom type has been reported for this species (Friele, 1902; Lemche, 1941a,b). The finding of a substan-
tial population of *C. nobilis* off the New Hampshire coast in October, 1974, marks the first time its presence has been noted on this coast since Verrill's original finding and has permitted studies to be done on its biology.

**Materials and Methods**

Specimens of *Coryphella nobilis* were collected from two locations by means of SCUBA. In 1971, one specimen was obtained in 20 meters of water from Flip Rock, southeast of Nahant, Massachusetts (42°24'N;70°55.5'W), but remained unidentified until November, 1974. Since October, 1974, a number of specimens have been observed and collected along the northeast coast of Smuttynose Island, Isles of Shoals, off the New Hampshire coast (42°59'N;70°37'W). The animals were returned to the University of New Hampshire, and maintained at 4° to 10°C in a closed, aerated sea water system. The animals were maintained on a diet of thecate hydrozoans: *Sertularia cupressina* Linnaeus 1758, and *Halecium articulosum* Clark 1875.

At intervals following each collection, animals were relaxed with 8% MgCl₂ and fixed in Hollande's variation of Bouin's fixative (Humason, 1967) for serial sectioning and microdissection. The serial sections were prepared using Steedman's (1960) polyester wax.

Radular slides were prepared by either allowing the tissue to naturally decay away from the teeth or were
chemically cleaned using 10% NaOH. In either case the radulae were washed, stained with Biebrich scarlet or acid fuchsin, and mounted in CMC-10 (Turtox). After several days, the edges of the coverslips were sealed with balsam; this prevented the formation of air bubbles while not adversely affecting the aqueous mounting medium.

Specimens collected and identified by A. E. Verrill as Coryphella mananensis (Stimpson 1853) were borrowed from the Peabody Museum, Yale University, New Haven, Connecticut, and the Philadelphia Academy of Natural Sciences, Philadelphia, Pennsylvania. Several of these were dissected and radular slides prepared. Two additional specimens of an unidentified nudibranch collected by V. N. Edwards (19 August 1902) were also obtained from the Philadelphia Academy and treated in the same manner. One specimen collected from Eastport, Maine, and labelled by Verrill in 1863 as Eolis purpurea (Stimpson 1853), was obtained from the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts. Approximately twenty of Verrill's radular slides labelled C. mananensis were examined at the Peabody Museum and nine slides whose identification was questionable due to their deteriorated condition were reclaimed and examined at the University of New Hampshire. Another slide labelled Coryphella salmonacea (Couthouy 1838), was also similarly treated.

Recently collected specimens of Coryphella nobilis have been deposited at the Museum of Comparative Zoology,
Harvard University, Cambridge, Massachusetts (#288010) and the Smithsonian Institution, Washington, D.C. (USNM 749067).

Results

*Coryphella nobilis* Verrill 1880

Plate I and II

*Coryphella nobilis* Verrill 1880 p.388
*Coryphella mananensis*; Verrill, 1882 p.552
*Coryphella salmonacea*; Holm, 1886 p.158 (in part)

see Lemche 1941a p.28

*Coryphella sp.* (anonyma) Bergh 1900 p.31-32 (in part)

see Lemche 1941a p.28

*Coryphella sarsi* Friele 1902 p.12
*Coryphella verrucosa*; Odhner, 1926 p.27
*Coryphella rufibranchialis*; Lemche, 1929 p.21

Geographic Distribution

Lemche (1941a,b) listed *C. nobilis* as a panarctic species with a boreal-submergent distribution. It has been reported from the northeast coast of North America (Cape Cod, Massachusetts to Eastport, Maine), East and West Greenland, Iceland, the Faroes, the Barents Sea, and the northern coast of Norway.
Description

This large (40-50mm) nudibranch has a translucent white body with maroon to red-brown cerata with conspicuous white tips. Its general body form is long, moderately tall and slender with the numerous cerata evenly distributed and held tightly and flattened over the dorsum. There are a few scattered white specks on the back posterior to the centrally located pericardium. These white pigment spots also form a stripe which extends down the entire length of the long pointed tail. The translucent oral tentacles are long, slender and evenly tapered and bear numerous white pigment spots on their distal tips which gradually decrease in number proximally. They are held forward, at a 45-50 degree angle to the main axis of the body. The relatively small head is narrower than the foot, and bears an oval mouth ventrally. The eyes and buccal mass can easily be seen even in larger animals through the dorsum of the head. The tan rhinophores are longer than the oral tentacles, evenly tapered, and tipped with white pigment spots. Superficially, they appear wrinkled and roughened, but under closer examination appear very heavily covered with small papillae or warts (Plate II).

The well developed anterior foot corners are held outstretched as the animal crawls over the substrate and each is equal to or greater in length than the width of the foot. A prominent groove is found along the anterior
margin of the foot and extends into the foot corners.

The non-clustered cerata are lanceolate in shape and have a central core composed of digestive gland epithelium. They are attached in oblique transverse rows to a prominent notal brim with the smallest cerata occurring on the lateral edge and the longest closest to the midline.

The genital orifice is located in the anterior quarter of the body, well below the notum. The anus (pleuroproct) is located in the anterior half of the body very high up on the right side of the body wall but distinctly below the notal brim.

The jaws are large and oval. The masticatory border contains several rows of flattened denticles along the entire edge (Fig. 1). The tips of these denticles are often broken and therefore appear bicuspidate. The radula formula is 20-22 X 1:1:1. The rachidian teeth are fairly broad with a low central cusp and 8-11 lateral denticles on each side. The lateral teeth are triangular, large, and bear 9-13 denticles on their median border. The lateral edge of the base bears a long posterior projection while the medial edge extends below the denticles as a shorter projection (Fig. 2).
Reproductive Anatomy

The reproductive system is composed of two functional units (Fig. 3). The largest is the ovotestis which in a mature animal can comprise 30 to 40% of the visceral mass. The second unit contains the accessory male and female glandular organs and occupies 20% of the visceral mass.

The ovotestis or hermaphroditic gland is located in the dorsal portion of the body cavity just under the dorsum and never extends ventrally into the foot. The organ is composed of many small arborescent follicles whose outline shows prominent lateral bulges. These bulges indicate the peripherally restricted development of oocytes. The follicles are loosely organized and bound together into larger lobes or bundles by a fibrous connective tissue sheath. This sheath also envelopes and holds together the entire ovotestis. The main posterior ceratal duct and its rami-fying branches penetrate the center of the entire organ.

Emanating from the base of each follicle is a small efferent ductule which conducts both sperm and ova that are simultaneously produced in a fully mature follicle. The

1. I feel the reproductive terminology used by Ghiselin (1965), is both anatomically and functionally descriptive and has therefore been used here.
ductules in each lobe join together into small ducts which eventually anastomose into the large main hermaphroditic or pre-ampullary duct. The pre-ampullary duct is located immediately dorsal to the main posterior liver duct for its entire course through the ovotestis. It expands into the ampulla as it passes anteriorly from the ovotestis to lie on the posterior left side of the nidamental (or female) gland complex. The ampulla loops back upon itself several times (up to nine loops) before passing anteriorly and deeper into the gland complex.

The end of the ampulla narrows sharply into the post-ampullary duct which penetrates into the nidamental gland complex between the lobes of the mucous gland (left) and albumen gland (right). This duct terminates in a junction located in the anterior medial portion of the gland complex. This junction marks the end of the common coelomic gonoduct and the beginning of the separate male and female pallial gonoducts. A short vas deferens exits from the left side of the junction and immediately expands into a prostatic region: an extremely thickened tube which loops two to three times above the anterior left side of the gland complex. The terminal end of the prostate narrows sharply into a highly muscularized ejaculatory duct which enters the posterior dorsal surface of the penial sac and extends to the tip of the penis. The penial sac contains a large expandable preputium and the long narrow tubular penis. Both preputium and penis exit through the
anterior portion of the common gonopore.

The proximal oviduct emerges from the right side of the junction and immediately turns posteriorly to lie beside the post-ampullary duct and terminal portion of the ampulla. Midway along its length the oviduct expands into a modified serial receptaculum seminis (spermatocyst). It then continues as the distal oviduct which, after making one loop, enters into the albumen gland. The albumen gland comprises approximately one quarter of the nidamental gland complex and is located in its right anterior side. In cross-section, its four horizontal folds resemble a four-leafed clover. Posteriorly this gland communicates with the membrane gland which is located along the entire posterior portion of the gland complex. The membrane gland communicates with the largest portion of the gland complex, the mucous gland. This gland can be divided into two sections. The first is a series of three vertical folds which are located on the extreme left side of the gland complex. This vertical triad communicates anteriorly with two horizontal folds which comprise the second section. It is this section which exits laterally by way of the nidamental duct to the gonopore. Proximally, the nidamental duct exists only as a common atrium between the median edges of the glandular tissue folds of the albumen, membrane and mucous glands. It becomes recognizable as a distinct duct just prior to the gonopore. The large spherical bursa copulatrix (spermatheca) lies wedged between the
lobes of the albumen and mucous glands and overlies the oviduct and receptaculum seminis. Its long narrow duct enters dorsally into the nidamental duct a short distance from the gonopore. Therefore, the distal portion of the nidamental duct serves both as a copulatory canal and as a canal for depositing the egg ribbon.

The egg mass is composed of long, thin (0.5-0.6mm) undulating coils (Type B; Hurst, 1967), the stroma containing hundreds of singly encapsulated eggs. Eggs average 80 μm in diameter and contain little yolk material while the oval capsules average 130 μm long by 100 μm wide. Egg masses reared under laboratory conditions (8-10°C) developed to planktotrophic veligers with Type I spiralled shells (Thompson, 1961) in 10-14 days.

Biology

Coryphella nobilis appears to have an annual life cycle. Large but immature specimens were collected in the fall (October-November) through mid-winter (January). Animals that were collected in January and maintained at ambient temperature with ample food (thecate hydroids) began to differentiate sexually by late April. This maturation may have been triggered by the increase in water temperature. In the field, a few egg masses and several small animals were collected on stalks of Tubularia sp. in early August. The reproductive season apparently spans from May to August, with the peak period in June and July.
correlating with the summer increase of *Tubularia* spp. populations.

During the fall and winter the animals were observed crawling and feeding upon the thecate hydrozoans *Halecium articulatum* and *Sertularia cupressina*. During the summer their diet also included athecate *Tubularia* species. Regardless of prey, the animals fed by biting off the entire polyp. In all cases, the hydroid species listed above were the dominant food source available to *C. nobilis* during each respective season. In New England, *C. nobilis* appeared to be restricted to cobble bottoms and rock ledges having a moderately rich epifauna and to depths greater than 20 meters.

**Museum Material**

Analysis of A. E. Verrill's radula slides labelled *Coryphella mananensis* indicated the majority were actually *Coryphella nobilis* (Table I-1). The only exceptions were four slides prepared by Verrill from animals collected south of Cape Cod, Massachusetts, in Long Island Sound (10207; 10208; 10387; 10388) (see Verrill, 1881, p.409). One such slide (10387) bore the label *Coryphella miniata mananensis?*. Verrill's own indecision about the identification is further reinforced by a note on the slide indicating he made a colored drawing of the animal. All these slides actually bear radulae of *Coryphella stellata* (Stimpson 1853). The radula slide (#12) identified as
C. salmonacea was in fact C. nobilis as was specimen #2595 from Harvard labelled Eolis purpurea. The two unidentified nudibranch specimens collected by V. N. Edwards and obtained from the Philadelphia Academy of Natural Sciences (#85630) were also C. nobilis.

Discussion

Literature concerning C. nobilis, as with the majority of coryphellids, is confused and needs clarification. Verrill's original description stated the rhinophores of C. nobilis were thickly covered with "small conical papillae or warts", and the lateral radula teeth were adenticulate along the "slightly wavy, uneven inner edge". Bergh (1900) described two specimens from the Danish Ingolf-Expedition, figured the radulae and masticatory border of the jaws, but only identified the specimens as Coryphella sp. (anonyma) Bergh 1900. From the "Michael Sars Expedition", Friele (1902) described a new coryphellid species (included a radula diagram) under the name C. sarsi Friele 1902. Odhner (1926) misidentified several specimens of C. sarsi sent to him by Roberg as C. verrucosa, but after publishing an excellent description of C. sarsi in 1929, corrected this error in 1939. Lemche (1936), after examining material sent to him by Bergh, concluded Coryphella sp. (anonyma) was in part C. sarsi. But in 1941a,b, after further examination of the literature and material available, he synonymized all forms of C. sarsi to C. nobilis.
Verrill 1880, based upon the following criteria: warded rhinophores, closely set cerata, and similarly shaped radula teeth. From the evidence available there can be no doubt Lemche is correct in his synonymies and animals collected off the New Hampshire coast are indeed *C. nobilis*. Verrill's type specimen with its adenticulated lateral teeth most certainly represents an aberrant form. As for Verrill's misidentification of *Coryphella mananensis* (Stimpson 1853), there can be no certain explanation. Stimpson described this species as having clustered cerata and wrinkled dorsal tentacles (rhinophores). Several others (Gould and Binney, 1870; Balch, 1909; Johnson, 1915, 1934; La Roque, 1953; Morse, 1969; Meyer, 1971) have synonymized Stimpson's form with the variety *rufibranchialis* (Johnston 1832) of *C. verrucosa* (Sars 1829). Based upon the description of *C. mananensis* and its marked differences from *C. nobilis*, there is little doubt Verrill erred in his interpretation of Stimpson's species. This would explain Verrill's contention that *C. mananensis* was a separate species and not a variety of *rufibranchialis* (see Balch, 1909, p.36) and that *C. mananensis* could be separated from *C. nobilis* by the former's highly denticulated lateral teeth.

The reproductive anatomy of *C. nobilis* resembles *C. verrucosa rufibranchialis*, (Odhner, 1939), *C. parva* Hadfield 1963, *C. lineata* (Alder & Hancock 1846), (Schmekel 1970) and *C. pedata* (Montagu 1815), (Odhner, 1939), regard-
ing the shape of the bursa copulatrix and its insertion on the dorsal surface of the nidamental duct. The reproductive system of *C. pedata* from the Mediterranean Sea, as figured by Schmekel (1970), does not resemble Odhner's diagram. Schmekel diagrammed two receptacula seminis, inserted by a common stalk into the oviduct and no bursa whatsoever. This extreme intraspecific variation has never been reported and has not been observed in any of the six New England coryphellids. This leads one to question whether the two forms of *C. pedata* are not perhaps different species. The presence of two bursae inserting into the oviduct has been reported by Miller (1971), for *C. albomarginata* Miller 1971. But he also noted a small round fertilization chamber (receptaculum seminis) slightly proximal to the two bursae. The Mediterranean form of *C. pedata* probably has a greater affinity to *C. albomarginata* than to the Norwegian form of *C. pedata*.

The mid-oviducal location of the receptaculum seminis in *C. nobilis* is also consistent with several other coryphellids. *C. v. rufibranchialis*, *C. trilineata*, and *C. lineata* all possess a receptaculum in this position. Odhner's diagram (1939) of *C. v. rufibranchialis* omits the receptaculum but I have confirmed its presence. MacFarland (1966) stated the spermatheca (actually receptaculum) in *C. trilineata* was round and entered the oviduct by a short duct. Personal dissections of several specimens of *C. trilineata* indicated the receptaculum was very elonga-
ted and without a separate duct. For this same species, Marcus (1961), while not figuring a receptaculum reported the oviduct stored sperm. The Mediterranean form of C. pedata is the only coryphellid reported thus far which has two distinct receptacula sharing a common stalk and inserting into the proximal oviduct.

Schmekel (1970) stated species with a diaulic reproductive system possess only receptacula and that bursae are restricted to triaulic species. Histological analyses of all six New England coryphellids which are diaulic indicate they definitely possess both a proximal receptaculum (for the long term storage of embedded exogenous sperm) and a distal bursa copulatrix (for the initial reception of non-oriented exogenous sperm and prostatic secretions). At no time were sperm found embedded or oriented in any manner in the distal vesicle. Personal dissections of many coryphellid species including many from widely distributed populations have revealed the position and insertion of the bursa copulatrix and receptaculum seminis to be very stable characters. Although their shape may change during sexual development and in pre- and post-copula animals, their general position and insertion point do not. Intraspecific reproductive differences reported here are considered either to be omissions or errors by the original investigators (i.e., C. v. rufibranchialis, C. trilineata) or to be outside the normally observed variations and therefore highly significant (i.e., the two forms of C.
pedata.

The ecological data collected on C. nobilis affect many of Lemche's assumptions (1941a,b). C. nobilis cannot be considered strictly a panarctic species. With its reproductive season in New England occurring in late spring and early summer (warmer water) and with its free swimming larval stage, this species more closely resembles the boreal-arctolittoral species C. v. rufibranchialis. Both species have a similar amphiatlantic distribution and their reproductive seasons correspond exactly in New England and probably in Greenland and Europe also (Lemche, 1921, 1941b; Bruce, Colman & Jones, 1963). The reproductive season of C. nobilis is opposite to the winter (cold water) spawning, direct-developing (Thompson's Type III, 1967) species C. salmonacea with which it has been allied (Franz, 1970).

The habitat characteristics for this study are congruous with the reported physical data (Verrill, 1880; Odhner, 1907; Lemche, 1941b) although the depths are considerably shallower. The nudibranch is associated with the epifauna at these depths. The reported hydroid prey species of C. nobilis fulfill all three of Swennen's (1961) criteria for a food species. All the compiled ecological data indicate this species has an annual life cycle. While this is contrary to the general life cycle groupings for hydroid feeding nudibranchs proposed by Miller (1962) and Thompson (1964), closer analysis indicates that although the prey species do exhibit their own seasonality, there is a
constant food supply available for a eurytrophic predator. Like \textit{Dendronotus frondosus} Ascanius 1774, (Miller, 1961; Thompson, 1964), \textit{C. nobilis} changes its prey species from thecate hydroids during the winter to a larger athecate hydroid in late spring and summer. This prey preference change to a species with larger (increased biomass), more energetically rich polyps, results in a net increase in energy gained per unit feeding time. This demonstrated feeding behavior which maximizes the net caloric intake per individual nudibranch correlates well with the theoretical model proposed by Emlin (1966, 1968). Field observations indicated the population densities of \textit{C. nobilis} did not reach sufficient numbers to have stabilized either the thecate or athecate hydroid populations. This is contrary to the conditions presented by Murdoch (1969) for predators switching prey species and contrary to my observations on fouling communities where nudibranch predators do regulate and stabilize hydroid population densities. The predatory behavior of \textit{C. nobilis} represents another example of the functional response "Type 2" (invertebrate) proposed by Holling (1959), where the impact of predation rises at a continually decreasing rate and produces a net decrease in the percentage of prey mortality with increasing prey densities. Thus any major change in the hydroid population is largely determined by changes in the physical parameters rather than by predation (Sanders, 1968).

The change in diet also corresponds closely to the
onset of sexual maturity. By synchronizing reproductive maturity with an abundant food supply, the animal greatly increases the chance that its metamorphosing larvae will encounter a stable food source and survive. It should be noted, however, that laboratory animals began sexual differentiation when maintained at ambient temperatures and on a diet of thecate hydroids. If the 10-14 day development time displayed by C. nobilis were coupled with a relatively short planktonic larval stage, it would allow metamorphosed larvae to utilize Tubularia as a food source for an initial period of rapid growth. This supposition is supported by my finding small immature specimens feeding on Tubularia in August and large yet sexually immature animals feeding on Halecium articulosum in October and November. Studies like those done by Thompson (1958, 1962), Tardy (1962), and Hadfield and Karlson (1969) on the induction of larval metamorphosis would be extremely beneficial to prove this hypothesis. Also, further studies should be conducted to elucidate whether the onset of sexual maturity is dependent upon the summer rise in temperature, the abundance and type of food supply, or a combination of these factors.

Summary

1. Finding Coryphella nobilis off the New Hampshire coast has allowed the first biological study of this nudibranch.
2. A literature review reveals that C. sarsi Friele 1902, and C. sp. (anonyma) Bergh 1900, are junior synonyms of C. nobilis Verrill 1880.

3. A study of A. E. Verrill's radula slides indicates animals reported by him as C. mananensis (Stimpson 1853), are actually C. nobilis. Verrill's type specimen of C. nobilis differs from Verrill's designated C. mananensis specimens only by the former's lacking a denticulated medial edge on the lateral teeth and this difference is not significant.

4. A functional proximal receptaculum seminis and a distal bursa copulatrix occur in this diaulic species.

5. Ecological data suggest this species has an annual life cycle, feeds on both thecate and athecate hydroids and has a boreal-arctolittoral distribution.

Literature Cited


Paris 254:2242-2244.


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<td>C. <em>salmonacea</em> Eastport (1864)</td>
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Plate I

Fig. 1. Ventral view of an anaesthetized specimen of **Coryphella nobilis** Verrill 1880, illustrating expansive notal brim, position of gonopore and anus, acute foot corners, and head morphology (scale=2.0mm).

Fig. 2. Right lateral view of same animal illustrating ceratal arrangement (scale=2.0mm).
Plate II

Enlarged view of a single rhinophore illustrating its warty or papillate surface (scale=0.25mm).
Fig. 1. Diagram of one jaw plate, with an enlarged representation of the denticulated masticatory border (scale=0.1mm).
Fig. 2. Radula diagram illustrating a central rachidian tooth and one pair of lateral teeth (scale = 0.02mm).
Fig. 3. Diagrammatic representation of the reproductive system: a, ampulla; alb, albumen gland; bc, bursa copulatrix; bw, body wall; d-ov, distal oviduct; g, common gonopore; j, junction; me, membrane gland; mu, mucous gland; ni, nidamental duct; ot, ovotestis; po-a, post-ampullary duct; p-ov, proximal oviduct; pr-a, pre-ampullary duct; pr, prostatic vas deferens; ps, penial sac; rs, receptaculum seminis (scale = 1.0mm).
CHAPTER II

CORYPHELLA VERRILLI SP. NOV. FROM NEW ENGLAND,
WITH A DISCUSSION OF THE GENERA
CHLAMYLLA, CORYPHELLA AND PARACORYPHELLA
(GASTROPODA: OPISTHOBRANCHIA).

Abstract

The external morphology, reproductive anatomy and
general biology of a new coryphellid nudibranch are given.
Its taxonomic position is discussed in relation to the
rare and little known species of Coryphella reported from
arctic regions of the Eastern and Western Hemispheres. A
new name, Coryphella zinfandella, is given to the specimens
Bergh (1886) misidentified as Gonieolis typica M. Sars 1861
while the genus Chlamylla Bergh 1886 is proposed as a
junior synonym of the genus Coryphella Gray 1850. The
validity of the genus Paracoryphella Miller 1971 is also
discussed.

Introduction

Records indicate that from 1877 to 1883, A. E.
Verrill collected several nudibranchs which he referred
to the genus Coryphella but not to species. In 1882, and
again in 1884, he published one of these findings, listing
it as a new but unnamed species. Bergh (1886) erected the
genus *Chlamylla* on the basis of a single specimen, *Chl. borealis* Bergh 1886, collected during the voyage of the "William Barents" to the Barents Sea. Also collected on this journey were three specimens which Bergh identified as *Gonieolis typica* M. Sars 1861. Later, Bergh (1900) provisionally referred two additional specimens to the genus *Gonieolis* under the names *G. intermedia* Bergh 1900, and *G. atypica* Bergh 1900. These animals were collected from the Davis Strait (West Greenland) during the Danish "Ingolf-Expedition". Odhner (1907) after describing a new species of *Gonieolis* placed that genus in the family Dendronotacea (now in Arminacea (Odhner, 1939)) and referred all Bergh's species of *Gonieolis* to the genus *Chlamylla*. Løyning (1932), after identifying a specimen of *Chl. intermedia* from the East Siberian Sea, suggested all of Bergh's species be synonymized under the name *Chl. borealis*. He also questioned maintaining the genus *Chlamylla* separate from *Coryphella*. Lemche (1941) followed Løyning's suggestion and considered all the presently known species under the name *Chlamylla borealis* Bergh 1886. The discovery off the New England coast of a population of large nudibranchs which bore a resemblance to Bergh's *Chlamylla atypica* and had a radula similar to Verrill's unnamed coryphellid species prompted a study of this nudibranch's biology and a review of the generic characters separating *Chlamylla* and *Coryphella*. 
Materials and Methods

Numerous specimens of *C. verrilli* n. sp. were first collected in August 1971, in the vicinity of Flip Rock, southeast of Nahant, Massachusetts (42°24'N;70°55.5'W). During May and June each year since 1974 small numbers of animals and egg masses have been collected in Gosport Harbor, Isles of Shoals, 10 kilometers off the New Hampshire coast (42°59'N;70°37'W). They were collected by means of SCUBA from depths of 20 to 30 meters. In August, 1975, three small specimens were obtained by otter trawl from an area east of the Shoals in 24-28 meters depth. The animals along with egg masses were returned to University of New Hampshire, kept at 4-6°C in a closed aerated sea water system and maintained on a diet of the athecate solitary hydrozoan, *Corymorpha pendula* Agassiz 1862.

Animals for microdissection and serial sectioning were first anaesthetized in 8% MgCl₂ and sea water, and then fixed in Hollande's cupripicri-formol acetic fixative. Serial sections were prepared using Steedman's (1960) polyester wax. Histochemical analysis of the female gland mass was done using a modified aldehyde fuchsin-alcian blue (pH 2.5) staining sequence (Spicer and Meyer, 1960). Egg masses collected in the field as well as those laid in the laboratory were maintained at 4-6°C in culture dishes and development followed until the veligers hatched.
Radular slides prepared by A. E. Verrill, borrowed from the Peabody Museum, Yale University, New Haven, Connecticut, were restored and examined. Additional nudibranch specimens collected off Block Island, Rhode Island (41°10'N; 71°35'W) (26–28 meters depth) and provisionally identified as Coryphella salmonacea (Couthouy 1838) by Dr. W. Hartman were also borrowed. Specimens of coryphellid nudibranchs collected by Verrill and preserved in alcohol were obtained on loan from the National Museum of Natural History, Smithsonian Institution, Washington, D. C.

Bergh's holotypes of Chlamylla borealis, Chlamylla intermedia and Chlamylla atypica loaned from the Universitetets Zoologiske Museum, Copenhagen, Denmark, were examined including the intact reproductive system of Chl. intermedia. An additional specimen of Chl. intermedia (#D-157, Zoologisk Museum, Oslo, Norway) reported from the "Maud" Expedition by Løying (1932) as well as the three syntypes of Coryphella islandica Odhner 1937 (loaned from the Danish Zoological Museum) were also examined. Included in the type material of C. islandica were Odhner's radular and jaw preparations (E-58) used in the original species description. An entire but dissected buccal mass from the second specimen was found within a separate vial. This buccal mass was placed in 10% NaOH overnight, the radula and jaw plates were then cleaned, stained and mounted for microscopic examination. The reproductive systems of the two previously dissected specimens were examined. The
third specimen was left untouched according to the wishes of Dr. Henning Lemche and is hereby designated as the lectotype.

The holotype of Coryphella verrilli has been deposited at the U. S. National Museum of Natural History, Smithsonian Institution, Washington, D. C. (USNM#749077) and a paratype at the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (#288375). Both the holotype and paratype were collected from Gosport Harbor, Isles of Shoals, off the New Hampshire coast.

Results

Coryphella verrilli n. sp.
Plate III, Fig. 1

Coryphella sp. Verrill, 1882, 1884
Coryphella sp. Bush, 1885

Geographic Distribution

Verrill (1882) reported this species from waters southwest of Gay Head, Martha's Vineyard, Massachusetts (39°59'N;70°06'W) and, in 1884, he listed its depth range as 30 to 168 fathoms. Analysis of Verrill's radula slides from the years 1877 to 1882 reveals that this species was collected from the St. Lawrence River (Murray Bay), Eastport, Maine, off Cape Ann and south of Cape Cod, Massachusetts. Hartman (1975, personal communication) has collected this nudibranch off Block Island, Rhode Island.
The type locality is now designated the Isles of Shoals, off the New Hampshire coast.

**Diagnosis**

Body broad, flattened; rhinophores ponderous, wrinkled, longer than the smooth oral tentacles; head oval, half of the foot width; anterior foot margin grooved, rounded; cerata crowded, non-clustered, in rows on prominent notum; anus in middle of right side just below notum (pleuroproctic); gonopore on right side at level of rhinophores; diagonally projecting cutaneous tissue fold located between gonopore and anus; radula triseriate, tapering, with 12–17 teeth rows; rachidian teeth with large, broad central cusp and 12–20 irregular lateral denticles; lateral teeth spatulate, non-denticulate; jaws oval, masticatory border long, with numerous fine denticles.

**Description**

Adults 40–65mm in length. Body opaque white, tan epidermal pigments on head, oral tentacles, rhinophores, and pericardium; cerata and notum with red-brown hepatic tissue, cnidosac white. Body shape broad, width exceeding height, gradual taper to short, pointed tail.

Oral tentacles long, evenly tapered, originate flush with anterior head border, directed anteriorly in wide "U" shape. Rhinophores wrinkled, bases thick, evenly tapered, longer than or equal to length of smooth oral
tentacles. Head oval, smaller than foot width, with oval, subterminal, ventral mouth. Anterior foot margin round, deeply grooved, producing distinct anterior labium; groove and labium extend posteriorly to level of gonopore; lateral foot margin extends beyond dorsum as distinct apron (Plate IV, Fig. 1,2).

Cerata numerous, non-clustered, borne on prominent notal brim; ceratal rows most numerous and compact anteriorly, in oblique rows of 5-7 cerata/row; lateral cerata small and slightly anterior to larger medial cerata, flattened anterioposteriorly, tip with large prominent cnidosac. Hepatic tissue within notum imparts dominant coloration, lines secondary ceratal branches, and associated series of plicated, hepatic diverticula; extensions of diverticula into cerata (Fig. 4). Common genital papilla on right side below notum, within anterior quarter of body; male opening anterior to female. Abanal cutaneous tissue flap, projects laterally, extends diagonally downward and posteriad from dorsal surface of genital papilla. Anus located on right side, just below notum in center of body length (pleuroproctic). Renal pore just anterior (2-3mm) to anus (Plate IV, Fig. 1).

Jaws long, oval; masticatory border prominent, extending approximately half total jaw length; cutting edge serrated with numerous rows of finely papillate denticles (Fig. 5). Radula small compared with entire buccal mass, tapered with newly formed teeth 3-5 times larger
than oldest teeth; formula equals 12-17 X 1:1:1 (mean 14 rows/n=7). Rachidian teeth with broad, strong, central cusp with 12-20 lateral irregular denticles; posterior edge of massive buttress as broad apron, articulates with base of preceding tooth. Lateral teeth spatulate, non-denticulated; bases large, with distinct arches for attachment onto radular membrane, anterior margin of bases thins rapidly into flattened distal portion of teeth (Fig. 6).

Reproductive Anatomy
(Fig. 7)

Ovotestis tan, large (comprising 50-60% of entire visceral mass), composed of many large compact lobes consisting of 4-7 smaller bundles of many small gametogenic follicles; follicles with papillate outer surfaces from bulging of peripherally developing oocytes. Small efferent ductules emerge basally from each follicle; transport both sperm and ova which are produced simultaneously in sexually mature individuals. Ductules merge into larger ducts which in turn anastomose at various intervals with large, main hermaphroditic or pre-ampullary duct (terminology after Ghiselin, 1965). Pre-ampullary duct lies dorsal to main liver duct, both traverse center of ovotestis; pre-ampullary duct coils, widens into ampulla at anterior edge of ovotestis. Ampulla long, straight, wide, passes anteriorly between lobes of mucous gland (left) and albumen gland (right); narrows into post-ampullary duct near anterior
edge of nidamental (female) gland complex. Post-ampullary duct moderately long, extends to right side and dorsally to horizontal component of mucous gland; terminates in junction which marks end of common coelomic gonoduct and beginning of separate male and female pallial gonoducts. Vas deferens emerges from right side of junction, expands into long, coiled nodular prostate; distal end abruptly narrows into ejaculatory duct. Ejaculatory duct long, coiled muscular; enters posterior end of penial sac, passes through eversible preputium to tip of conical penis.

Proximal oviduct moderately wide, inner epithelial lining plicated; emerges from left side of junction, turns posteriad, loops behind post-ampullary duct, passes right and dorsally toward albumen gland and enters ventrally into semi-serial receptaculum seminis (spermatocyst). Receptaculum moderately large, sacculate, muscular, located just anterior to lobes of albumen gland; inner epithelial lining highly diverticulated, with dense numbers of embedded exogenous sperm. Distal oviduct emerges somewhat ventrally from terminal end of receptaculum; epithelium plicated with embedded exogenous sperm along entire length; enters into androgenic portion of nidamental duct distal to functional bursa copulatrix (spermatheca). Bursa consists of thin-walled pouch in right side of nidamental duct just distal to albumen gland; in post-copula animals contains large bolus of unoriented sperm, several ova in varying steps of dissolution and weakly acidic mucopoly-
saccharide secretions from albumen gland. Albumen gland with 6-8 large interconnected tissue folds, located in medial and right side of nidamental gland complex; communicates directly with membrane gland. Membrane gland located along entire posterior portion of gland complex, glandular folds undergo transition into mucous gland. Mucous gland in two distinct portions, proximal portion makes up left side of gland complex, composed of three nearly vertical lobes; distal portion forms floor of anterior gland complex, consists of two horizontal lobes, distal lobes exit via nidamental duct and female gonopore. Nidamental duct exists proximally as ill-defined channel or cavity, borders delineated by medial projections of glandular tissue folds, distal portion as distinct canal to exterior; medial dorsal wall of distal portion plicated, separates duct in two, anterior portion for ovopositioning, distal portion of androgenic function for penis and exogenous sperm reception during copulation.

Egg mass white to pink, tall wavy ribbon standing on edge (Type A, Hurst, 1967) (Plate III, Fig. 2); usually deposited around base and stalk of hydroid prey, also on any suitable firm object. Stroma with several thousand egg capsules (diameter=875 μm), each contains 30-50 non-yolky eggs (diameter=70-80 μm); develop into planktotrophic veligers with spiralled, Type I shells (Thompson, 1961) in 20-30 days at 6°C.
Biology

Off southern Maine and New Hampshire, *Coryphella verrilli* appears to have a subannual life cycle. Its presence correlates with the annual spring appearance of its hydroid prey, *Corymorpha pendula*. Small (10-20mm) but sexually mature nudibranchs were collected in May (1974, 1975) and in August (1975). Large (40-65 mm) animals were found in June (1975) and August (1971). In the laboratory, well-fed animals held at ambient temperatures (4-6°C) increased their body length by 2.5 to 3.0 times in one week. Starvation reversed this process with little loss of sexual activity but the rate of decrease was much slower and less dramatic. A 2mm juvenile collected unnoticed with specimens of *C. pendula* developed to sexual maturity within 25 days and reached 28mm in length. This suggests the small sexually mature animals collected in August (1975) were the progeny of adults which laid egg ribbons in May and early June and not necessarily the result of a minimal food supply.

*Coryphella verrilli* feeds on its hydroid prey by first using the jaws to rip off the tentacles, and then the entire polyp. If food is plentiful, the nudibranch then proceeds to another hydroid and thus allows the first to regenerate, but, if food is limited, the animal will devour the entire stalk starting with the distal end and
progressing to the base.

Collection sites off New Hampshire and Massachusetts were similar physically; the bottom composed of crushed shell fragments mixed with silty sand and temperatures ranging from 5-8°C at depths of 20-25 meters. Except for the much shallower depths, these data agree with those given by Verrill (1882).

Museum Material

Table II-1 lists the numbers of Verrill's radular slides and one of W. Hartman's that were determined to be Coryphella verrilli. Three radular slides ( #'s 10609; 10613; 10698) were extracted from specimens on file at the U. S. National Museum of Natural History (USNM #'s 382282, 382284, 382293, respectively). A fourth specimen (USNM #382324) identified as Coryphella nobilis Verrill 1880 by Verrill and later identified as Coryphella stimpsoni (Verrill 1879) by Nils Odhner (1932, unpublished) is actually Coryphella verrilli. From the information available, Verrill's specimen #10609 (USNM #382282) is the one Verrill designated and reported as Coryphella sp. in 1882. All eleven radular slides from the museum material agree both in the number of radular teeth rows (mean=14.4 rows) and in tooth morphology with representatives of Coryphella verrilli. However, the lateral teeth on five of Verrill's radulae showed degrees of slight denticulation on the inner margins.

The distinctive abanal cutaneous tissue fold was
present on the right side of three of Verrill's preserved specimens. The fourth (USNM #382324) was so badly preserved that its presence was impossible to confirm. All four specimens possessed a rounded and grooved anterior foot margin and contained a large amount of hepatic tissue within the notum.

Bergh's holotype of *Chlamylla borealis* had at one time been allowed to dry out, hence little additional information was gained beyond Bergh's original description. However, it was possible to note the prominent notum did not project more than in some other coryphellids and the surface of the one remaining but detached rhinophore was covered with small tubercles or warts which were especially numerous basally. The specimen of *Chlamylla atypica* had been dissected by Bergh and the entire visceral mass removed. However, as the external body wall was intact, it was possible to see the expansive notum with numerous rows of non-clustered cerata and containing much hepatic tissue, the rounded, deeply grooved anterior foot margin, the highly wrinkled rhinophores (nearly twice the length of the oral tentacles) and on the right side, a distinct abanal cutaneous tissue fold which extended anteriorly to form the dorsal surface of the preputium. The one jaw plate in the specimen vial had a long masticatory border (equal to half the jaw length) with 2-5 rows of small flattened denticles.

The holotype of *Chlamylla intermedia* had also been
dissected by Bergh, but the distal genital organs and a portion of the ovotestis were found intact and are represented schematically in Figure 8. The ampulla was slightly coiled at the proximal end but its main portion consisted of a smaller straight tube located along the left side of the female gland complex. At its distal end, the ampulla narrowed rapidly into a long, thin post-ampullary duct which terminated at the junction where the male and female portions of the reproductive system separated. A short vas deferens emanated from the junction's right side and expanded rapidly into a highly coiled, nodular prostatic portion. The distal end of the prostate narrowed abruptly into a long, coiled muscular ejaculatory duct which entered the posterior end of a very small penial sac and continued to the distal tip of a long, thick conical penis. The moderately thick, muscular, slightly coiled oviduct emerged from the left side of the junction and laid along and just under the main body of the ampulla. It was shiny white, filled with sperm (most likely exogenous) and its terminal end entered directly into a moderately large sac-like swelling. This structure had a direct connection to the female gonopore via the distal nidamental duct and also communicated posteriorly with the albumen gland. This sac must serve as a functional bursa copulatrix while the oviduct itself must also serve as a functional receptaculum seminis. The warty rhinophores were nearly twice the length of the smooth oral tentacles. The grooved anterior
foot margin projected posterio-laterally into small foot auricles. Contrary to Bergh's report, the pleuroproctic anus was located in the middle of the body length while the renal pore was located more anterior to the anus than in *Chl. atypica*. The notum was also expansive, bore the many rows of non-clustered cerata and contained only a moderate amount of hepatic tissue.

The "Maud" specimen of *Chl. intermedia* differed in its reproductive anatomy from the holotype in several respects. In Lødyning's specimen, the small, conical penis emerged from a large eversible preputium. Also, while the proximal portion of the oviduct was narrow, distally it was greatly expanded and almost bulbous (functional receptaculum seminis). It entered medially and without narrowing into a large saccular bursa copulatrix.

Examination of the syntypes of *C. islandica* revealed the oral tentacles to be longer than the smooth rhinophores in the two dissected specimens. However, the situation was reversed in the lectotype. The anterior foot margin was grooved and expanded laterally into moderately acute foot auricles in all three specimens, while the notum was very prominent and projected out quite far from the body. The anus was located approximately in the middle of the right side (pleuroproctic) and well below the notum. Odhner's (1937) diagram of the reproductive system was essentially correct except he omitted the oviduct and receptaculum seminis (Fig. 8). The proximal oviduct emerged from the
junction as a moderately long duct. Distally it expanded into a large bulbous structure; the receptaculum seminis. The oviduct then continued as the very short distal oviduct and inserted directly into the nidamental gland complex in the area of the albumen gland. Odhner's radular slide (E-58) did indeed contain a radula with an accessory series of lateral teeth on the left side. The accessory series had a separate insertion onto the radular membrane and could be independently separated from the usual series of lateral teeth. The radula from the second specimen entirely lacked a separate accessory series, but the lateral series on the left side possessed strongly bifid teeth, the second cusp emerging from the outside basal edge. The right series of lateral teeth of the first radula had broad, crescent shaped cusps arising from moderately large bases, while most of the right lateral teeth of the second radula had short, blunt and somewhat malformed cusps. The entire radula in both cases was tapered with the youngest (newly formed) teeth being approximately 1.5-2 times larger than the oldest. The rachidian teeth of both radulae were wide with the buttress deeply incised. The articulating apron of the leading edge was not particularly large or expanded. In all cases, the long broad central cusp was bifid and laterally flanked by 5-7 cuspidate denticles.
Discussion

The suborder Aeolidacea has been postulated to be of monophyletic origin arising from the Dendronotacea (Tardy, 1970). This evolutionary step is thought to be mediated by the genus Notaeolidia Eliot 1905 (Eliot, 1905; Vayssière, 1906; Odhner, 1934, 1944), with most higher aeolids arising from the genus Coryphella Gray 1850 (Odhner, 1939). This hypothesis is strengthened and Ghiselin's (1965) argument of a polyphyletic origin refuted when the morphology of the little known species Chlamydia borealis, Chl. intermedia, Chl. typica, Chl. atypica, as well as Coryphella verrilli are considered. The genus Notaeolidia is characterized by a large, broad, flattened body; anterior foot margin rounded and grooved; anus pleuroproctic, located in middle of body; notum wide, undulate, bearing one or more rows of non-clustered cerata; digestive gland lobed, flocculent mass within body cavity, with ramifications into body wall forming thick spongy layer within notum before extending into cerata; jaws oval, non-denticulate masticatory borders; radula with strongly cuspidate rachidian teeth, 2–5 pairs of denticulated lateral teeth. The six congeners of Notaeolidia display phylogenetic trends of radula and digestive system simplification. N. gigas Eliot 1905, has 4–5 pairs of lateral teeth with a large portion of digestive tissue within the body cavity.
and a single row of cerata along the notum. *N. rufopicta* Thiele 1912, however, has a reduced radular formula of two pairs of lateral teeth and a greatly simplified digestive system containing most of the hepatic tissue within the liver ducts and cerata.

*Chlamylla borealis*, *Chl. typica*, *Chl. intermedia*, *Chl. atypica* and *Coryphella verrilli* retain many of the primitive characters demonstrated within the *Notaeolididae*. They possess the broad, flattened body form, the expansive notum bearing numerous non-clustered cerata and all have a spongy layer of hepatic tissue within the notum. *Chl. atypica* and *C. verrilli* still retain the round anterior foot margin, while *Chl. borealis*, *Chl. intermedia* and *Chl. typica* have developed slight foot auricles. The anus is pleuroproctic in all the species and is located medially in *Chl. intermedia*, *Chl. atypica* and *C. verrilli*, but slightly more posterior in *Chl. borealis* and *Chl. typica*. The jaws of *Chl. borealis* retain the primitive adenticulate condition while *Chl. atypica*, *C. verrilli*, *Chl. intermedia*, and *Chl. typica* respectively, have progressively increased the amount of denticulation. The radula morphology of *Chl. typica* with the long, thin median cusp of the rachidian and its highly denticulated lateral teeth most nearly approximates the radulae demonstrated within the *Notaeolididae*. The other species show progressive loss of radular denticulation with *Chl. intermedia* and *C. verrilli* having denticulated rachidian teeth and smooth
laterals while *Chl. borealis* has lost all denticulation on both the rachidian and laterals. Within the reproductive systems of these species there is again a demonstrated phylogenetic progression of advancement from the Notaeolididae (Fig. 8). Only the reproductive systems of *N. gigas* and *N. subgigas* have been described and only in limited detail (Vayssière, 1906; Odhner, 1944). Vayssière (1906) stated that the oviduct of *N. gigas* was thick and highly plicated internally. Also, the small, sessile bursa copulatrix was located near the penial sheath and communicated with the oviduct as well as the genital opening. This is nearly the exact condition found in *Chl. intermedia*. In *Chl. borealis*, the bursa is large with a short duct, while in *Chl. typica*, the bursal duct has elongated and opens into the mucous gland near the gonopore. Bergh did not describe the oviduct of *Chl. borealis* but figured a simple oviduct entering into the female gland mass (Bergh, 1886, pl. 3, fig. 25). In *C. verrilli*, the bursa has moved internally, being located proximal to the opening of the oviduct into the female gland mass and the oviduct has expanded to form a distinct receptaculum seminis. An internal movement of the bursa into the gland mass would better allow the reception of the large bolus of sperm needed to fertilize the tremendous numbers of eggs produced by this species. It would also reduce the need for multiple matings. The congested area immediately proximal to the gonopore in most coryphellid species
would not readily accommodate such an increased space requirement. The only alternative would be to increase the bursal stalk length thus carrying the bulbous portion of the bursa internally where it would have more expansion room. The bulbous receptaculum seminis of this species increases the available surface area needed for the storage of increased sperm numbers. The nodular and expanded prostatic portion of the vas deferens found in all these species is again congruous with the need for producing large numbers of sperm.

The reproductive anatomy of *Chi. atypica* remains uncertain. The seminal vesicle and duct described and figured by Bergh (1900, pl. 5, fig. 1g,h) could either be the receptaculum seminis and oviduct similar to *C. verrilli* or the bursa and its stalk as in *Chi. typica* or *Chi. borealis*. The distal oviduct (i.e. functional receptaculum) and distinct saccular bursa copulatrix of Løying's "Maud" specimen are likely to be intermediate between *C. verrilli* and the holotype of *Chi. intermedia*. These differences appear to be real and not just intraspecific variations. None of the specimens of *C. verrilli* examined (two serial sectioned, and four microdissected) approached the condition in the "Maud" specimen. However, a specimen presently in the author's collection of an unidentified coryphellid collected off the coast of Nome, Alaska, matched the oviduct, receptaculum, bursa, and penis morphology found in the "Maud" specimen. It may well be that the "Maud" and
Alaskan specimens are conspecific and a species separate from Bergh's *Chl. intermedia* and *C. verrilli*.

Bergh (1886) defined the genus *Chlamylla* as follows: body elongated with short tail; notum prominent or projecting; foot wide with anterior angles produced; jaws with non-denticulated masticatory border; radula triseriate, lateral teeth denticulated; prostate elongated; penis unarmed. The broad flattened body shape is common to *Coryphella islandica*, *C. falklandica* Eliot 1907, *C. salmonacea* (Couthouy 1838), and *C. borealis* Odhner 1922. A prominent and projecting notum comparable to that found in the presently described *Chlamylla* species is also found in *Coryphella parva* Hadfield 1963, and *Coryphella nobilis* Verrill 1880, as well as in all the above mentioned species.

In addition to the flattened body and wide notum, *Coryphella athadona* Bergh 1875, also possesses a round anterior foot margin. All coryphellids possess the anterior foot groove. Although Gray (1850) defined the genus *Coryphella* as having "gills in tufts" and the designated type species *C. rufibranchialis* (Johnston 1832) [=*C. verrucosa* M. Sars 1829] has clustered cerata, Bergh (1864) placed *Aeolis salmonacea* Couthouy 1838, with non-clustered cerata in the genus *Coryphella*. Several congeners, namely *C. nobilis*, *C. fusca* O'Donoghue 1921, and *C. stellata* (Stimpson 1853), demonstrate progressive degrees of ceratal clustering and reduction and breakup of the notum. Personal observations have revealed there is also a gradual loss of the spongy hepatic
tissue within the notum which is concomitant with a pro-
gressive containment within the primary and secondary
hepatic ducts and ceratal core (C. islandica, C. borealis,
C. falklandica, C. salmonacea, C. stellata, and C.
verrucosa Sars 1829, respectively). The majority of cory-
phellids have some degree of denticulation on the masti-
catory border of the jaw plates, but it is entirely lack-
ing in C. parva. All coryphellids have triseriate radulae
with varying degrees of denticulation on the rachidian
and lateral teeth. The distinctive nodular prostate
common to most Chlamylla species is also found in Coryphella
cynara Marcus and Marcus 1967 as well as Dendronotus iris
Cooper 1863 (MacFarland, 1966) and Flabellina babai
Schmekel 1970, but is lacking in Chl. typica (see Bergh,
1900, footnote 11). An unarmed penis is common to all cory-
phellids. It is therefore apparent that as defined by
Bergh, the genus Chlamylla possesses no unique characters
distinctive from Coryphella, nor do the congeners actually
demonstrate any.

I therefore propose to relegate Chlamylla Bergh
1886 a junior synonym of Coryphella Gray 1850 with the
following taxonomic changes at the species level:

1. Coryphella atypica (Bergh 1900), Nov. Comb.

Gonieolis atypica Bergh 1900. p.37. (Davis Strait,
66°43′N;55°57′W).

Chlamylla atypica (Bergh). Odhner, 1907. p.33.
Chlamylla borealis (Bergh). Lemche, 1941. p.25
[In synonymy only.]

2. CORYPHELIA BARENTSI VAYSSIÈRE 1913. p.2

Coryphella salmonacea 'Couthouy' G. O. Sars 1878. p.319. (northern Norway); non salmonacea Couthouy 1838.

Coryphella verrucosa (M. Sars). Ohdner, 1907. p.86;
Ohdner, 1922. p.32 [Identification in error.]

Coryphella borealis Ohdner 1922. p.31 (Vadsø, Norway);
non borealis Bergh 1886.

3. CORYPHELIA BOREALIS (BERGH 1886), NOV. COMB.

Chlamylla borealis Bergh 1886. p.9 (Barents Sea, 75°49'N; 53°41'E); non borealis Ohdner 1922
[= C. barentsi Vayssière]

4. CORYPHELIA INTERMEDIA (BERGH 1900), NOV. COMB.

Gonieolis intermedia Bergh 1900. p.36 (Davis Strait,
66°43'N; 55°57'W).

Chlamylla intermedia (Bergh). Ohdner, 1907. p.33.

Chlamylla borealis (Bergh). Lemche, 1941. p.25 [In synonymy only.]

5. CORYPHELIA ZINFANDELLA N. NOM.

Gonieolis typica 'M. Sars' Bergh 1886. p.13. (Barents Sea, 69°45'N; 54°34'E); non typica
M. Sars 1861.

Chlamylla typica (Bergh). Ohdner, 1907. p.33.
Formally there is no species named *Gonieolis typica* Bergh 1886 because the three specimens in question were misidentified by Bergh as being *G. typica* M. Sars 1861, and Odhner's (1907) transfer of the species to *Chlamylla* also does not validate the name *Chl. typica* (Bergh 1886). The description of Bergh's specimens is complete enough to leave little doubt they are a valid species and I therefore propose to rename it *Coryphella zinfandella*. The epithet *zinfandella* was chosen strictly in an effort to apply a totally unrelated name to this congener and for its euphonic nature. The name therefore has no biological significance. *C. zinfandella* cannot be allied to any of Bergh's other *Chlamylla* species based on several differences (Table II-2). The masticatory border of the jaws bear 4-5 rows of distinct denticles unlike the other species. The radular morphology is also distinct both in numbers of rows of teeth and rachidian and lateral teeth morphology. It is distinct reproductively by possessing a spherical bursa with a long narrow stalk and by lacking the nodular prostate. The holotype of *Coryphella intermedia* and many specimens of *C. verrilli* in the same size class as *C. zinfandella* all have the nodular prostate and in *C. verrilli* the prostate is nodular in immature specimens so it is not a case of Bergh's specimens being immature. The lack of the nodular prostate is also reinforced by the fact that although Bergh had three specimens, he indicated no major variations between
them. The only species which resembles *C. zinfandella* is *Coryphella polaris* Volodchenko 1946. The two appear very similar in external morphology but *C. polaris* has only 17 radular teeth rows and the rachidians differ by the latter's possessing an acutely pointed, bifurcated central cusp. The lateral teeth of both species appear nearly identical. Both species are rare and further comparisons must await additional collections in the typelocalities.

*Coryphella borealis* (Bergh 1886) must be maintained for it differs on several counts from the others. In *C. borealis*, the rhinophores are inserted far apart while in the other species they insert next to each other. There is a strong wing-like projection at the posterior edge of the gonopore in *C. borealis*, and the base of the pear-shaped penis bears small, soft tubercles and short villi. The masticatory border of the jaw and the radular teeth are all described as smooth. The wing-like projection on the gonopore may be a fixation artifact and the smooth radular teeth may be an individual variation but because there are no other specimens known, Bergh's description must stand intact.

*Coryphella intermedia* (Bergh 1900) also appears to be a valid species. Bergh described distinctly projecting foot corners for this species and noted the degree was more than any of his other species. This character is notably absent in Løyning's "Maud" specimen which has a
round anterior foot margin. The very broad and obtusely
tapered rachidian teeth of *C. intermedia* with their short,
rather narrow central cusp are distinctive; so also are
the wide, obtusely triangular lateral teeth with their
short, non-denticulated cusps. The reproductive system
also shows characters unique from the others including the
"Maud" specimen (i.e. the long oviduct which lacks a
separate bulbous receptaculum seminis, small penial sac
with projecting long conical penis and lack of an expandable
preputium). The holotype was sexually mature, and there­
fore the lack of these reproductive structures cannot be
attributed to immaturity. This also applies to *C.
intermedia* lacking the abanal projecting cutaneous tissue
fold present in *C. atypica* and *C. verrilli* and the wing­
like posterior extension of the gonopore in *C. borealis*.

The "Maud" specimen of *C. intermedia* appears to
be distinct from Bergh's holotype based upon its longer,
more pointed cusp on the rachidian and longer, more acute­
ly pointed lateral teeth (non-denticulate, however). It
has a short oviduct with a bulbous receptaculum seminis,
a saccular bursa and a large penial sac which contains
a large eversible preputium from which emerges a very
small conical penis. Løyning (1932) while noting the
similarity between the "Maud" specimen and Bergh's *C.
atypica* (including the similarly shaped preputium and
penis) assigned the specimen to *C. intermedia* because it
lacked the longitudinal fold of *C. atypica* and possessed
smooth lateral radular teeth like *C. intermedia*. Løyning did not examine the internal reproductive anatomy of the "Maud" specimen and it is these structures that present the strongest case for keeping the two species separate. The "Maud" specimen most closely resembles *Coryphella stimpsoni* var. *incognita* Derjugin 1926 (=*C. barentsi* Derjugin 1924, non-Vayssière 1913). Both animals agree in external morphology including possessing a round anterior foot margin and a large eversible preputium with a small conical penis. There is also a greater similarity in radular morphology between the "Maud" specimen and Bergh's *C. intermedia*, despite the slightly denticulated lateral teeth of *C. incognita*. Unfortunately, the internal reproductive anatomy of *C. incognita* remains undescribed but, in light of the above listed similarities, I propose to redesignate Løyning's "Maud" specimen to *C. incognita* Derjugin 1926. Also included in this designation is the author's specimen collected off Nome, Alaska. The varietal name *incognita* must be raised to the specific level because this species significantly differs from *Coryphella stimpsoni* (Verrill 1879).

The closest similarity between any of these species exists between Bergh's *C. atypica* and *Coryphella verrilli*. Both possess the distinctive abanal projecting cutaneous tissue fold. In *C. atypica* however, it is very expansive and forms the majority of the upper lip of the gonopore and preputium. In *C. verrilli* it is prominent only in the area between the gonopore and anus. The longitudinal
fold of \textit{C. verrilli} is consistently present in all the author's specimens, A. E. Verrill's specimens and those of W. Hartman. Its presence does not appear to be size related for it occurred in specimens ranging from 10-65mm in length. All, however, appeared to be near or completely sexually mature, but so were all of Bergh's specimens and Løyning's "Maud" specimen. The tissue fold does therefore, in my opinion, constitute a valid diagnostic character for these two species. \textit{C. atypica} and \textit{C. verrilli} can be separated on radular characteristics. Bergh stated the radula of \textit{C. atypica} possessed 25 rows of teeth with marks visible on the lower (oldest) end of the radula indicating 8 rows had fallen off; total 33 rows. Radular slides of 7 \textit{C. verrilli} specimens collected by the author indicated a range of 12-17 rows of teeth (mean=14.4) (four slides had 9-11 rows and were considered incomplete). All the radulae were dissected from specimens within the size range of Bergh's \textit{C. atypica}. Therefore the fact that \textit{C. atypica} has at least twice as many radular teeth must be considered significant and diagnostic. The radular morphology is also distinctive for \textit{C. atypica} and \textit{C. verrilli}. The base of the rachidian teeth of \textit{C. verrilli} is broader and more ponderous than \textit{C. atypica}; the central cusp shorter and wider. The lateral teeth of \textit{C. verrilli} are broader, more spatulate and non-denticulated while in \textit{C. atypica} they are narrower, longer, sharply denticulated basally and the distal end of the cusp hooks inward. It
must also be noted however, that the lateral teeth on five of Verrill's radular slides possessed slight denticulations basally. Also, the type locality of C. atypica (Davis Strait, West Greenland) is 20° latitude north of Newfoundland, the northernmost area recorded where Verrill collected at least one specimen of C. verrilli. The two species, C. atypica and C. verrilli, may be synonomy, but based solely upon Bergh's description of the only specimen of C. atypica, there appears to be sufficient evidence to describe C. verrilli as a new species. What remains to be done is to resample the type locality for C. atypica and then compare representatives of each.

From personal observations of the syntypes, Coryphella borealis Odhner 1922 (=C. salmonacea G. O. Sars 1878, non-Couthouy 1838) (D-16103, D-16110, Zoologisk Museum, Oslo, Norway), there is no doubt that Odhner was correct in designating as a new species specimens collected and identified by G. O. Sars (1878) as C. salmonacea. However, there is a high probability that this species is actually a junior synonym of Coryphella barentsi Vayssière 1913. Vayssière (1913) noted the radula of C. barentsi approached that of Coryphella sp. Bergh 1900 (pl. V, fig. 12), which Lemche (1936, 1938) designated as Coryphella gracilis (Alder & Hancock 1844). However, the radula morphology of C. gracilis (personal observations) does not match Bergh's diagram nor Vayssière's. From Vayssière's description and figure of C. barentsi there are signi-
significant similarities between it and Odhner's *C. borealis*. They agree in body form and size, head shape, foot morphology, ceratal insertion on an expanded notum, and possessing non-clustered cerata. Vayssière states *C. barentsi* has 27 radular teeth rows while Odhner (1939) lists a range of 24-31 for *C. borealis*. Both also agree within reasonable limits in jaw (including masticatory border) and rachidian and lateral teeth morphology including denticulation. In my opinion there is enough evidence to suggest the synonymy of these two species and that this action is preferable to introducing a new name for Odhner's *C. borealis* which is a mandated consequence of placing Bergh's *C. borealis* in the genus *Coryphella*.

Miller (1971) erected the family Paracoryphellidae and genus *Paracoryphella* based upon the type species *Coryphella islandica* Odhner 1937. Miller's criteria for the new designation was based upon the fact *C. islandica* lacks oral glands, has rhinophores of greater length than the oral tentacles and has a radular formula of 2:1:2. I have personally examined 12 coryphellid species for the presence of oral glands. Eight species lacked distinct oral glands including the type *Coryphella verrucosa* M. Sars 1829. There appear to be no natural lines of taxonomic division based upon presence or lack of oral glands among the coryphellids examined. The large rhinophores are not a valid generic criterion. In fact, only the lectotype of *C. islandica* possesses rhinophores longer than the oral
tentacles. In the other two syntypes, the oral tentacles are much longer, extending posteriorly to or beyond the gonopore. The length of the oral tentacles versus the rhinophores is highly variable among the Coryphellidae and is valid only at a specific level and only on live or properly relaxed and fixed specimens. The radular formula of 2:1:2 cannot strictly be given for C. islandica for on none of the two radular slides does there occur any sign of an accessory lateral teeth series on the right side. Although the lateral teeth of the first radula appear properly formed on both sides, the accessory now is not. The lateral teeth of the second radula are totally malformed; while the teeth on the left side have two cusps, the lateral teeth on the right side have essentially none. What remains to be done is to get permission to examine the lectotype and/or to collect more specimens. In my opinion, these radulae are aberrant and malformed and while they may represent a phylogenetic remnant further proof is needed before giving this character generic status. This argument is strengthened when C. islandica is analyzed for other coryphellid characters. Its body form, distinct foot auricles, oral tentacles and rhinophores indicate an advancement from Coryphella borealis (Bergh 1886), C. intermedia, C. atypica, C. incognita and C. verrilli. Although C. islandica has non-clustered cerata inserted on an expanded notum, there is less hepatic tissue within the notum than in the previously mentioned species including Coryphella barentsi and
C. falklandica. The distinct receptaculum seminis and distal saccular bursa with its short wide stalk, although still primitive, represents an advanced intermediate stage between the Notaeolididae and Coryphella zinfandella and forms like C. salmonacea and C. nobilis. Taking all these characters into account, it is not advisable to maintain the monotypic genus Paracoryphella Miller 1971 for an animal with distinct coryphellid characteristics and a suspect radular morphology.

Summary

1. Examination of A. E. Verrill's specimens and radular slides has revealed Coryphella sp. Verrill 1882, 1884 are identical with a recently collected unidentified nudibranch and is therefore named Coryphella verrilli.

2. The biology of C. verrilli indicates it is a stenotrophic predator feeding on a patchily distributed and seasonal hydroid prey, Corymorpha pendula.

3. Modifications of the reproductive system of C. verrilli (i.e., placement and form of the bursa and receptaculum seminis) represent an adaptation to produce large numbers of eggs necessary for survival on a patchy, unstable prey.

4. Characteristics displayed by congeners of Chlamyella Bergh 1886 do not significantly differ from those of Coryphella Gray 1850 and therefore this genus is relegated to a junior synonym status with appropriate
taxonomic changes.

5. Because of the incomplete radular data available for C. islandica Odhner 1937 and the fact this species possesses many major coryphellid characteristics, it is proposed to retain this species in Coryphella and not to maintain the monotypic genus Paracoryphella Miller 1971.

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adjacent parts of the Atlantic, consisting mostly of deep-sea species, with notes on others previously recorded. Conn. Acad. Sci., Trans. 6:139-294.

Table II-1

A. E. Verrill's Radula Slides of *Coryphella verrilli* n. sp.

<table>
<thead>
<tr>
<th>Slide#</th>
<th>Original Labelling</th>
</tr>
</thead>
<tbody>
<tr>
<td>10172</td>
<td><em>Holis papillosa</em> or <em>Galvina</em> Eastport, Me. (1870)</td>
</tr>
<tr>
<td>10323</td>
<td><em>Coryphella</em> sp. Murray Bay, Quebec, G. M. Dawson</td>
</tr>
<tr>
<td>10354</td>
<td><em>Coryphella</em> sp. off Cape Cod Sta. 364 (1879)</td>
</tr>
<tr>
<td>10609*</td>
<td><em>Coryphella</em> sp. off Martha's Vineyard Sta. 1038 (1881)</td>
</tr>
<tr>
<td>10613</td>
<td><em>Coryphella</em> sp. off Cape Cod Sta. 990 (1881)</td>
</tr>
<tr>
<td>10616</td>
<td><em>Coryphella</em> sp. off Martha's Vineyard Sta. 988 (1881)</td>
</tr>
<tr>
<td>10698</td>
<td><em>Coryphella</em> sp. Massachusetts Bay Sta. 169 (1878)</td>
</tr>
<tr>
<td>10705</td>
<td><em>Coryphella</em> sp. off Martha's Vineyard Sta. 1138 (1882)</td>
</tr>
<tr>
<td>10733</td>
<td><em>Coryphella</em> sp. Mass. Bay, off Salem Sta. 32-33 (1877)</td>
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W. Hartman's Radula Slide of *Coryphella verrilli* n. sp.

15603  | *Coryphella* ?*salmonacea* off Block Is., R. I. Sta. 12 (1967)                      |

Table II-2
Comparison Chart of Species Characteristics

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>C. articulata</th>
<th>C. berthaei var. variecano</th>
<th>C. berthaei sp. nov.</th>
<th>C. berthaei sp. nov.</th>
<th>C. berthaei sp. nov.</th>
<th>C. berthaei sp. nov.</th>
<th>C. berthaei sp. nov.</th>
<th>C. berthaei sp. nov.</th>
<th>C. berthaei sp. nov.</th>
<th>C. berthaei sp. nov.</th>
<th>C. berthaei sp. nov.</th>
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<tbody>
<tr>
<td><strong>Body Shape</strong></td>
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<tr>
<td>Broad, flattened</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
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<td>Elongate, narrow</td>
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<td><strong>Notum</strong></td>
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<tr>
<td>Prominent, continuous</td>
<td>x</td>
<td>x</td>
<td>x</td>
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<td>Round</td>
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<td>Rousene, non-clustered</td>
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<td><strong>Digestive Gland Epithelium</strong></td>
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<tr>
<td>Notum &amp; Cerata</td>
<td>x</td>
<td>-</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
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<td>Cerata only</td>
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<tr>
<td>Anterior half</td>
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<td>x</td>
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<td>Middle</td>
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<td>Posterior half</td>
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<td>x</td>
<td>x</td>
<td>x</td>
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<td><strong>Masticatory Border, Jaws</strong></td>
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<td>Denticulation (harticulation)</td>
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<td>Fine</td>
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<td><strong>Radula</strong></td>
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<td># teeth rows</td>
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<td>27</td>
<td>17</td>
<td>24-31</td>
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<td>Denticulation, rachidians</td>
<td>13-15</td>
<td>7</td>
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<td>8-9, 16</td>
<td>9-13</td>
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<td>Penis (shape)</td>
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<td>pear</td>
<td>?</td>
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<td>Preputium</td>
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<td>?</td>
<td>villi</td>
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<td>x</td>
<td>x</td>
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<td>nodular</td>
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<td>smooth</td>
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Plate III

Fig. 1. Dorsal view of living *Coryphella verrilli* illustrating head and body morphology (scale=5mm).

Fig. 2. Egg mass of *C. verrilli* laid in the laboratory upon natural substrate (scale=5mm).
Plate IV

Fig. 1. *C. verrilli*: right lateral view of preserved specimen illustrating rounded anterior foot margin (f) and labium (l), gonopore with everted preputium (p), cutaneous tissue fold (ctf) and anal papilla (a) (scale=5mm).

Fig. 2. *C. verrilli*: ventral view of same preserved specimen illustrating head morphology and rounded anterior foot margins (scale=5mm).
Fig. 4. *C. verrilli*: diagram of hepatic duct arrangement in notum; stippled areas indicate hepatic tissue: 
a, primary ceratal duct; b, secondary duct; c, hepatic diverticulae; d, ceras; e, cnidosac
(scale=0.5mm).
Fig. 5. *C. verrilli*: diagram of one jaw plate, with enlargement of masticatory border and its finely papillate denticulation (scale=0.5mm).
Fig. 6. *C. verrilli*: radula diagram illustrating one tooth row: a, lateral tooth ventral view; b, rachidian; c, lateral tooth dorsal view (scale=0.025mm).
Fig. 7. *C. verrilli*: diagram of reproductive system: a, ampulla; alb, albumen gland; an, anal papilla; bc, bursa copulatrix; bw, external body wall; ctf, cutaneous tissue fold; ej, ejaculatory duct; g, common gonopore with everted preputium and conical penis; j, junction; me, membrane gland; mu, mucous gland; ni, nidamental duct; ov, oviduct; ot, ovotestis; po-a, post-ampullary duct; pr-a, pre-ampullary duct; pr, prostate gland; ps, penial sac; rs, receptaculum seminis (scale=1.0mm).
Fig. 8. Hypothesized representation of the reproductive advancement of some primitive Coryphellidae from the Notaeolidae: hypothetical ancestor represents a composit of Notaeolidia gigas and N. subgigas (labelling as Fig. 7; p, penis; pu, preputium).
To other Coryphellidae

Coryphella verrilli n. sp.

Coryphella islandica Odhner 1937

Chlamydia intermedia (Bergh 1900)

Chlamydia typica (Bergh 1886)

Hypothetical Ancestor

Fig. 8
CHAPTER III

THE TAXONOMY AND BIOLOGY OF
FOUR NEW ENGLAND CORYPHELLID NUDIBRANCHS
(GASTROPoda: OPISTHOBRANCHIA)

Abstract

The taxonomy and description of four coryphellid nudibranchs (Coryphella gracilis, C. pellucida, C. salmonacea and C. verrucosa) found within the Gulf of Maine is presented. Their distribution, seasonality and prey preferences within this area are discussed relative to the European data. The ecology and coexistence of these and two other coryphellid species are discussed in terms of their dominance of the New England nudibranch fauna.

Introduction

Early literature on the New England aeolid family Coryphellidae, consisting principally of new species descriptions and distributional records was summarized by Gould & Binney (1870). Verrill (1879-1882) added additional species while greatly increasing the data on their distributions. This literature served as a basis for the checklists of Johnson (1915, 1934). Moore (1964) and Meyer (1971) included partial reviews of several coryphellid species while Franz (1970, 1975) and Meyer (1971) discussed their
zoogeography. However, there has been no comprehensive review of the taxonomy and biology of the genus Coryphella in New England. Kuzirian (in press) gives a detailed account of Coryphella nobilis Verrill 1880 in New England and also reports on a new coryphellid species Coryphella verrilli (manuscript submitted). The purpose of this report is to review the four other known New England coryphellids and to discuss the mechanisms which allow these six closely related species to coexist.

Materials and Methods

From 1972 until 1976 the following sites in the Gulf of Maine were sampled regularly: East Point, Nahant, Massachusetts (42°24'N;70°54'W); the Isles of Shoals, off the New Hampshire coast (42°59'N;70°37'W); Portsmouth Harbor, New Hampshire (43°04'N;70°42'W); York, Maine, (43°10'N;70°35'W) and the Eastport Maine area (Cobscook Bay, Bay of Fundy) (44°53'N;66°59'W). The Portsmouth Harbor site was sampled at least monthly while the remaining sites were sampled seasonally. The nudibranchs were collected both intertidally at minus low tides and subtidally to depths of 33 meters by SCUBA. Field data included recording physical parameters (i.e. temperatures at depth and substrate type) for each site, direct observations on their feeding behavior and prey species selected and the presence of spawn. The nudibranchs were returned to the University of New Hampshire and maintained at
ambient temperatures in either a closed, aerated, or recirculating sea water system. Development of egg masses collected in the field or deposited in the laboratory was followed and development times at specific temperatures noted. Where specific prey items were unclear, either squash preparations of cnidosacs were examined for nematocyst contents and/or gut contents analyzed.

Results

Coryphella gracilis (Alder & Hancock 1844)
Plate V, Fig. 1, 2

Eolis gracilis Alder & Hancock 1844. p.166 (Cullercoats, England)

Eolis smaragdina Alder & Hancock 1851. Pt. 5, Fam. 3, pl. 17, fig. 1 (Whitely, Northumberland, England)

Coryphella gracilis (A & H). Alder & Hancock, 1855.
Pt. 7, p.49

Coryphella smaragdina (A & H). Alder & Hancock, 1855.
Pt. 7, p.49

Eolis stellata Stimpson 1853. p.25 (Grand Manan, Canada)

[In synonymy.]

Coryphella mananensis (Stimpson). Verrill, 1881. p.409
[Name in error, see notes.]

Coryphella rufibranchialis (Johnston). Bergh, 1885.

p.51 [In synonymy.]

Coryphella lineata (Loven). Johansen, 1902. p.387;
Lemche, 1936. p.26


*Coryphella frigida* Grieg 1907. p.538 (78\(^\circ\)09'N;14\(^\circ\)01'W)

[East Greenland]

*Coryphella rufibranchialis* var. *clavigera* Odhner 1929. p.10 (Bjarkö, Norway)


*Coryphella verrucosa verrucosa* (M. Sars). Thompson & Brown, 1976 p.148 [In synonymy.]

Geographic Distribution

In the western Atlantic, *Coryphella gracilis* occurs from south of Cape Cod (Verrill, 1881), north through the Gulf of Maine, to Nova Scotia (Meyer, 1971), and Newfoundland (Odhner, 1929); in the eastern Atlantic from Iceland, the Faroes, the British Isles, Denmark, France and the Mediterranean (Lemche, 1938).
Description

Adults 8-12mm in length (occasionally to 15mm). Body translucent to opaque white; cerata bright orange to crimson, distally tipped with white. Body form elongate, narrow, tapering to pointed tail. Oral tentacles, rhinophores and tail striped with white pigment spots.

Oral tentacles moderately long, thick basally but taper gradually to blunt tip, originate slightly posterior to anterior edge of oral surface; mouth located ventrally, usually with distinct "V"-shaped notch visible dorsally. Rhinophores smooth, thinly tapered; equal to or longer than oral tentacles. Foot auricles acute, length equal to or greater than foot width; anterior margin grooved, produces anterior labium, groove extends into foot auricles.

Cerata clustered (5-6 clusters for larger animals, 4-5 for smaller ones), borne on distinct notum (notum reduced but continuous between clusters); ceratal shape lanceolate. Genital orifice below posterior half of first ceratal cluster, just below notum; posterior rim often with projecting tissue flap. Penis and preputium long, tubular with conical tip. Anus always below first ceratal row of second cluster on right side (pleuroproctoc) (Plate V, Fig. 2); renal pore within interhepatic space.

Jaws oval, masticatory border prominent, with 3-4 irregular rows of denticles (Fig. 9). Radular formula
12-16 X 1:1:1 (mean=13 rows/n=8). Rachidian teeth broad, central cusp moderately long, flanked by 4-9 strong, lateral denticles. Lateral teeth distinctly sickle-shaped (concave inner margin), inner edge possessing 6-9 long, curved denticles; denticulation extends almost to distal tip of each tooth (Fig. 10).

Egg mass undulating spiralled coil (Type B; Hurst, 1967) when deposited on flat substrate; more commonly in undulating loops around stems and branches of hydroid prey. Eggs singly encapsulated, 50-60\(\mu\)m in diameter; development to planktotrophic larvae in 12-15 days at 12°C; veliger shell Type I (Thompson, 1961).

Occurrences

_Coryphella gracilis_ is found throughout the Gulf of Maine to depths of 33 meters, and almost exclusively associated with _Eudendrium_ spp. Occasionally, in deeper water (25-33m), when _Eudendrium_ is scarce, it has been observed feeding upon _Haleciun articulorum_ Clark 1875 and epizooic campanularid hydroids such as _Clytia johnstoni_ Alder 1857. In southern regions of the Gulf of Maine, _C. gracilis_ is most abundant and sexually mature during August and September. In northern Maine they are still moderately abundant and spawning in October and early November. Small numbers of sexually mature individuals plus egg masses have been collected in February and March while juveniles 1-2mm in length have been found in late April and May. These data
indicate *C. gracilis* probably has 2-3 generations per year and a planktonic larval stage lasting 6-8 weeks.

**Discussion**

*Coryphella gracilis* (Alder & Hancock 1844) was described from specimens collected in Cullercoats, England. In 1851, they described a similar species, *Eolis smaragdina* from Whitely, Northumberland, England. It differed from the former in having green cerata, a shorter head and more denticles on the rachidian teeth. Both species were placed in the genus *Coryphella* by Alder & Hancock in 1855. Eliot (1906) found animals collected in Plymouth, England to be intermediate both in color and radular dentition and suggested animals with green cerata be called *C. gracilis* var. *smaragdina*. Later, Eliot (1910) stated the color patterns were probably due to dietary differences and listed both color forms under the name *C. gracilis*.

*Coryphella gracilis* has been confused in the European literature with the morphologically similar species *Coryphella verrucosa* (M. Sars 1829). Trinchese (1881) and Vayssière (1888) included *C. gracilis*, *C. smaragdina* along with *C. pellucida* (Alder & Hancock 1843) and *C. rufibranchialis* (Johnston 1832) (=*verrucosa*, see below) as junior synonyms of *Coryphella landsburgii* (Alder & Hancock 1846) while Bergh (1885, 1890) listed all the above species under the name *C. rufibranchialis*. Odhner (1929) described *C. rufibranchialis* var. *clavigera* from animals collected off
Bjarkø, Norway. He stated this new variety was intermediate in form between the typical C. verrucosa and C. rufibranchialis. However, based upon Odhner's description of the animal's size, external morphology (including cerata inserting on a distinct notum) and radula morphology (see Odhner, 1929, fig. 7, p. 11) there can be no doubt that the animals he designated C. r. var. clavigera are actually C. gracilis.

Lemche (1936, 1938) attempted to differentiate between the species C. gracilis, C. borealis Odhner 1922 and C. bostoniensis Bergh 1864 (non-Couthouy 1838) but later (1941a, b) changed all his identifications to C. verrucosa after Odhner (1939) published his account on the latter species.

Bruce, Colman & Jones (1963) included C. gracilis as a variety of C. verrucosa. Thompson & Brown (1976) listed C. gracilis as a junior synonym of C. verrucosa verrucosa while maintaining C. smaragdina as a distinct color variety of C. verrucosa. Thanks to the cooperation of Mr. Bernard Picton (Ulster Museum, Belfast, Ireland), I have had the opportunity to examine preserved specimens and radular slides of specimens he designated C. gracilis and C. smaragdina. There is no doubt that the two species are identical for no differences could be found in their external morphology or radular characteristics. Eliot's (1910) conclusion that the color differences are dietary is correct. C. gracilis is also totally distinct from C. verrucosa, and the two are easily distinguished based upon the characters given in Table III-1. These characters
are extremely stable and have not been observed to overlap.

After examining the European examples of *C. gracilis* and reviewing Alder & Hancock's description, I am now convinced they are identical with specimens reported in the American literature as *Coryphella stellata* (Stimpson 1853) (Gould & Binney, 1870; Whiteaves, 1901; Johnston, 1915, 1934; La Roque, 1953; Franz, 1970). Meyer (1971) stated *C. gracilis* (probably citing Lemche, 1936, p.141) differed from *C. stellata* by the former's having the anus located below the third ceratal row of the second cluster. This was not the case in the specimens examined. *C. gracilis* consistently had the anus located below the first row of the second ceratal cluster. *C. verrucosa* has the anus located below the third ceratal row of the second cluster and Lemche (1941a,b) as stated earlier did redesignate as *C. verrucosa* specimens he originally identified as *C. gracilis*. The European examples of *C. gracilis* are identical in all major respects with the New England specimens designated *C. stellata* and are therefore listed as a junior synonym. The only difference noted was the European examples were sexually mature at a smaller size than those generally collected in the Gulf of Maine. This is undoubtedly due to ecological factors such as temperature and/or food sources. Dr. N. W. Riser (1976, personal communication), collected one small, sexually mature individual in the Eastport, Maine, area which appeared similar to the color variety *C. g. smaragdina* and agreed in radular dentition with
Alder & Hancock's diagram (Alder & Hancock, 1855, suppl., pl. 47, fig. 11) for C. gracilis.

Grieg's (1907) Coryphella frigida was based on a single specimen and the external morphology (including expanded notum), number of radular teeth rows, rachidian shape and dentition as well as the jaw and its masticatory border all fall within the limits of variation with C. gracilis. The lateral radular teeth agree with C. gracilis in their shape, but Greig described and figured them (pl. 79, fig. 15) as being adenticulate, a condition also found in a specimen (#49) collected in Eastport, Maine, and identified as Coryphella stellata by A. E. Verrill. One radular slide of C. gracilis prepared by B. Picton had adenticulate lateral teeth present on the right side while those on the left side were typically denticulated. Because of these examples, I feel the adenticulate lateral teeth of C. frigida represent an aberrant form of C. gracilis and that the other similarities between the two species are sufficient to list C. frigida as a junior synonym of C. gracilis.

Verrill (1881) reported specimens collected off Race Point, Cape Cod, Massachusetts, as Coryphella mananensis (Stimpson 1853). However, examination of four of the radular slides (#10207, 10208, 10387, 10388) indicates the animals were actually C. gracilis. Swennen (1961) listed specimens of Coryphella verrucosa in his report on the ecology of nudibranch molluscs occurring in the Netherlands. However, when the food preference and size data
given are coupled with the author's statement the animals appeared similar to *Eolis gracilis* Alder & Hancock, there can be little doubt the animals actually were *Coryphella gracilis*. The same is also probably true of an animal reported as *C. verrucosa* by Platts (1973) from County Down, Ireland, which was less than 7mm long and spawned in late April. This small size at sexual maturity and time of year for spawning better agrees with reports on *C. gracilis* than *C. verrucosa*.

The ecology and distribution of *C. gracilis* in the Gulf of Maine agree well with the reported European data (Beaumont, 1900; Walton, 1908; Lemche, 1929; Rasmussen, 1973) when differences in the hydroid fauna are taken into account. In the Gulf of Maine, *C. gracilis* has at least two generations per year. If the field data indicating a 6-8 week planktonic stage are correct, there is potentially time for a third generation. Intensive sampling during the late spring and early summer may give further evidence to support this hypothesis. Deep (25-33 meters) subtidal collection data suggest a small breeding population is maintained after the intertidal and shallow subtidal populations have disappeared. This population would provide a continuous source of larvae for new recruitment into the shallower areas when conditions were favorable. *C. gracilis* is rather stenotrophic in shallow waters. Adults, juveniles and egg masses have been found only on *Eudendrium* spp. In deeper water, however, where *Eudendrium* is not as plentiful, they
are more eurytrophic, feeding upon small epizoic campanularid hydroids.

**Coryphella pellucida** (Alder & Hancock 1843)

Plate VII, Fig. 1

**Eolis pellucida** Alder & Hancock 1843. p.243

(Cullercoats, England)


**Coryphella rutila** Verrill 1879. p.314 (Eastport, Maine, U.S.A)

**Coryphella landsburgii** (A & H). Trinchese, 1881. p.98

[In synonymy.]

**Coryphella rufibranchialis** (Johnston). Bergh, 1885.

p.51 [In synonymy.]

**Coryphella verrucosa verrucosa** (M. Sars). Thompson & Brown, 1976, p.148 [In synonymy.]

**Geographic Distribution**

In the western Atlantic, **Coryphella pellucida** occurs from south of Cape Cod, Massachusetts (Russell, 1964) northward throughout the Gulf of Maine (Verrill, 1879, 1882; Russell, 1935); in the eastern Atlantic, from the Faroes, Norway, Britain, France and the Mediterranean (Lemche, 1929; Ros, 1975).
Description

Adults 20-30 mm in length. Body translucent white; cerata crimson red, with white tips; oral tentacles, rhinophores with distal white stripe on upper surfaces. Body shape elongate, narrow, moderately tall (height=width); evenly tapered to pointed tail.

Oral tentacles long, bases moderately thick, evenly tapered; originate subterminally from dorsal head surface. Rhinophores thin, evenly tapered, to twice length of oral tentacles. Head small, distinctly narrower than foot width. Foot auricles long (equal to or greater than foot width), acutely pointed; anterior foot margin grooved to produce anterior labium; labium notched medially.

Cerata clustered (8-10), in rows, first cluster with 5-6 rows, remaining clusters with 1-2 rows each; rows on common stalk, stalk extension of notum; notum reduced between clusters. Genital openings separate, male orifice anterior to female; below center of first ceratal cluster, right side. Anus on right side in interhepatic space, just below notum (pleuroproctic).

Jaws oval, masticatory border moderately short, 3-4 rows of denticles (Fig. 11). Radular formula 30-40 X 1:1:1 (mean=36/n=6). Rachidian large, broad; central cusp short, 8-11 lateral denticles (often bicuspidate). Lateral teeth broad, base rectangular; cusp large, triangular,
on medial side, edge non-denticulate (Fig. 12).

Egg mass thin undulate coil (Type B; Hurst, 1967); eggs 70–80\(\mu\)m in diameter, singly encapsulated; development in 12–14 days at 8–10°C; planktotrophic veligers with spiralled, Type I shell (Thompson, 1961).

**Occurrences**

*Coryphella pellucida* has been collected consistently but in low numbers from New Hampshire to Eastport, Maine. It has been collected rarely along the Massachusetts coastline. Juveniles collected from late July to early November have been associated with *Eudendrium* spp. and *Tubularia* spp. Adults reach sexual maturity and spawn from April to early June. Within the Gulf of Maine, *C. pellucida* occurs from the low intertidal to at least 20 meters depth and always on hard, rocky substrates.

**Discussion**

Originally described as *Eolis pellucida* Alder & Hancock 1843, this species was transferred to *Coryphella* by M. Gray (1850). Verrill (1879) described *C. rutila* from specimens collected in Eastport, Maine, U.S.A., and stated this new species was closely allied to *Eolis pellucida*. Unfortunately, Verrill neither described nor figured the radula. The only radular slide of Verrill's labelled *C. rutila* (#10176) on file at the Peabody Museum is actually *Coryphella gracilis* Alder & Hancock 1843. However, Verrill's
description of C. rutila does not match that of C. gracilis. Recent specimens collected from the Eastport, Maine area which resemble C. rutila are unquestionably C. pellucida. When Verrill's description of the size, color, body and head shape, and ceratal arrangement of C. rutila are coupled with finding the almost identically described species, C. pellucida, in the type locality of C. rutila, it seems reasonable to assume the two species are identical. I have therefore included C. rutila as a synonym of C. pellucida.

As stated above, Trinchese (1881) included C. pellucida along with several other coryphellid species in the synonymies of Coryphella landsburgii (Alder & Hancock 1846) while Bergh (1885, 1890) included C. pellucida as a synonym of Coryphella rufibranchialis (Johnston 1832). These synonymies have since been rejected. Thompson & Brown (1976) included C. pellucida as a synonym of Coryphella verrucosa verrucosa. C. pellucida however is a distinct species easily distinguished from C. verrucosa based upon coloration, body and head morphology, ceratal arrangement and radular morphology (i.e. numbers of teeth rows, rachidian and lateral teeth shape and dentition).

Lemche (1929) listed C. pellucida from depths of 20-120 meters. Within the Gulf of Maine, this species has been collected intertidally to 20m depth on hard, rocky substrates only. The seasonal occurrence data indicate C. pellucida has an annual life cycle with spawning occurring in the spring, thus confirming reports by Russell (1935,
1964). Miller (1961) listed both thecate and athecate hydroids as prey species of *C. pellucida*. Within the Gulf of Maine *C. pellucida* has only been found feeding upon athecate hydroids (*Eudendrium* spp. and *Tubularia* spp.) even though thecate hydroids (principally *Hydra mania* sp. and *Sertularia* spp.) have also been present. In laboratory prey choice experiments, *C. pellucida* chose *Eudendrium dispar* over *Tubularia* sp. During the fall and winter, *Eudendrium* spp. was a dominant hydroid in the localities sampled and the one *C. pellucida* was associated with. During the spring however, when *Tubularia* spp. abounds, adults and egg masses of *C. pellucida* have been collected on and maintained in the laboratory on these hydroids.

*Coryphella salmonacea* (Couthouy 1838)

Plate VI, Fig. 1,2

*Doris papillosa* 'Muller', Fabricius, 1870. p.345. non-papillosa Muller 1776.

*Eolis* (Cavolina Brugière 1791) *salmonacea* Couthouy 1838
(Charles River, Massachusetts, U.S.A.)

*Aeolidia bodōensis* 'Gunnerus', Møller, 1842. p.78. non-bodōensis Gunnerus 1770

*Cavolina salmonacea* (Couthouy). DeKay, 1843. p.11


*Coryphella salmonacea* (Couthouy). Bergh, 1864. p.227

*Cuthona stimpsoni* Verrill 1879. p.314 (Eastport, Maine,
U.S.A.)

**Coryphella stimpsoni** (Verrill). Verrill, 1880. p.388

**Aeolis sp.** Holm 1886. p.156; Lemche, 1941a. p.26

**Cretena olrikii** 'Mørch', Posselt & Jensen, 1898. p.245

non-olrikii Mørch 1857; Lemche, 1941a. p.26 [In part.]

**Coryphella sp. (anonyma)** Bergh 1900. p.31; Lemche, 1941a p.26, 28 [One specimen]

**Coryphella stimpsoni** var. *laevidens* Knipowitsch 1902. p.391 (Stor Fjord, Spitzbergen)

**Aeolidia papillosa** (Linnaeus) Hågg, 1905. p.104; Lemche, 1941b. p.27

Geographic Distribution

In the western Atlantic, **Coryphella salmonacea** occurs within the entire Gulf of Maine north to Halifax, Nova Scotia (Verrill, 1880; 1882) and Greenland; in the eastern Atlantic from Iceland, Spitzbergen, the north coast of Norway, the Bering Sea (Lemche, 1938; 1941a,b) and within the Arctic Seas (Knipowitsch, 1902).

Description

Adults 25-40mm in length. Body opaque white, gonad sometimes imparts pinkish hue; cerata orange-tan to deep red-brown, distal tip with white ring; oral tentacles, rhinophores with distal white stripe; rhinophores often tan. Body shape broad, flattened (width exceeding height);
even taper to blunt tail; tail posterior to cerata.

Oral tentacles long, evenly tapered; originate subterminally from dorsal head surface; longer than rhinophores. Rhinophores wrinkled, evenly tapered, thinner than oral tentacles; bases widely separated; eyes posterior to rhinophores. Head shape oval to trefoil; mouth ventral, oval (relative to body axis). Foot auricles small, well posterior to anterior foot margin; grooved to produce anterior labium; groove extends into foot auricles; labium notched medially.

Cerata numerous, non-clustered, evenly spaced, lanceolate; 3-4 rows anterior to rhinophores; longest medially, shortest laterally. Notum continuous, expanded. Genital orifice lateral, right side below notum; anterior third of body. Anus right side, below notum (pleuroproctic), posterior two thirds of body length.

Jaws large, well-developed, triangular; masticatory border short, 4-5 rows of irregular denticles (Fig. 13). Radular formula 25-34 X 1:1:1 (mean=28 rows/n=32). Rachidian teeth moderately wide, central cusp long, acutely pointed; 8-12 strongly hooked lateral denticles. Lateral teeth acutely triangular or slender, bases large; denticulation variable, 0-15 with 8-12 most common; denticles basal half only (Fig. 14).

Egg mass thick, smooth, 2-4 whirls (Type B; Hurst, 1967); stroma with large, yolky, singly encapsulated eggs (240-250 μm in diam.). Development direct or contained
within egg mass; to crawling juveniles in 45-55 days at 4-6°C. Larval shell reduced, shed before hatching.

Occurrences

*Coryphella salmonacea* has been collected from Boston Harbor to Eastport, Maine. In Massachusetts, New Hampshire and southern Maine, the animals have occurred intertidally to depths greater than 20 meters on hard, cobbled bottom or rock ledge substrates. Sexually mature adults have been found in large numbers feeding and depositing egg masses upon the colonial tunicate *Amaroucium constellatum* Verrill 1871 from December to March. Small juveniles have been collected infrequently in late summer and early fall feeding upon available hydroid species (principally *Tubularia* spp.). In the Eastport, Maine area, large juveniles occur in September and early October on hard, rocky substrates and feed upon *Tubularia spectabilis* (Agassiz, 1862). Large numbers of mature adults plus a few egg masses have been collected consistently in late October and November. These nudibranchs were swarming over mud flats with no obviously available food source. In June, 1976, adults and egg masses were also collected in these same areas (Dr. M. P. Morse, personal communication).
Discussion

*Coryphella salmonacea* (Couthouy 1838) was originally described as *Eolis* (*Cavolina* Brugière) *salmonacea* from specimens collected in the Charles River, Massachusetts, U.S.A. It was formally placed in the genus *Cavolina* by DeKay (1843). Mørch (1857) cited *Aeolidia papilligera* Beck 1847 as a junior synonym of this species, to which he also identified *Doris papillosa*, (Fabricius, 1780) and *Aeolidia bodöensis*, (Møller, 1842) (non-Gunnerus 1770). These synonymies were first cited by Bergh (1864) when he transferred *Eolis salmonacea* to the genus *Coryphella* Gray 1850, and accepted by Iredale & O'Donoghue (1923) and Lemche (1941a).

Verrill (1879) described *Cuthona stimpsoni*, from specimens collected in Eastport, Maine, U.S.A., but in 1880, transferred it to the genus *Coryphella*. Verrill (1882) later noted its close alliance to *C. salmonacea*. Knipowitsch (1902) described a new variety, *C. stimpsoni laevidens*, based upon the slender, adenticulate lateral radular teeth. I have examined all of Verrill's paratype material on file at the U.S. National Museum of Natural History, Smithsonian Institute, Washington, D.C., as well as his radular slides kept at the Peabody Museum, Yale University, New Haven, Connecticut. Data from this material revealed Verrill collected specimens which he identified as *Coryphella stimpsoni* over the entire range known
for *C. salmonacea* (Table III-2). The only material remaining which Verrill identified as *C. salmonacea* was one radular slide and that actually bore the radula of *C. nobilis* (Kuzirian, in press). All of Verrill's paratype material compares favorably with specimens presently identified as *C. salmonacea*, including external and reproductive morphology, radular shape, dentition and numbers of teeth rows. It therefore seems appropriate to include *Coryphella stimpsoni* (Verrill 1879) as a junior synonym of *Coryphella salmonacea* (Couthouy 1838). The variety *C. stimpsoni laevidens* proposed by Knipowitsch (1902) is also invalid. Specimens of *C. salmonacea* collected within a single population normally display the full range of radular variation figured by Krause (1892) and Knipowitsch (1902).

The ecological data obtained for *Coryphella salmonacea* within the Gulf of Maine indicate this species has an annual life cycle. It spawns in the southern regions of the Gulf of Maine from December to March when the water temperatures are low. In the Eastport, Maine area, colder water temperatures occur earlier in the fall and extend further into spring. The continued low water temperatures probably account for finding mature adults and egg masses in June, 1976. The winter spawning under cold water conditions further supports Lemche's (1941b) statement that *C. salmonacea* is a panarctic species. Within the Gulf of Maine, the reproductive season of *C. salmonacea* compares favorably with data reported from Greenland and northern
Europe. However, Verrill's data indicating *C. salmonacea* is distributed south of Cape Cod in deep water suggest this species does have a boreal-submergent portion to its distribution. This species also appears to be more tolerant of higher temperatures as juveniles than Lemche (1941b) suggested because they have been collected in August and September when the water temperatures at depth are above 10°C.

On hard substrates in southern and northern regions of the Gulf of Maine, *C. salmonacea* feeds on hydroids (i.e. *Tubularia* spp.) as juveniles and the colonial tunicate *Amaroucium constellatum* as adults. This does not explain the behavior patterns of the animals consistently found in the fall swarming over mud flats in Eastport, Maine. Morse (1971) speculated these animals fed upon the abundant burrowing sea anemones, *Edwardsia elegans* Verrill 1869 and *Halcampa duodecimcirrata* (Sars 1851). However, in the areas sampled during this study, these anemones were not present in sufficient numbers to support the large nudibranch population which occupied the mud flats at this time of year. Squash preparations of the cnidosacs from these animals showed many stored nematocysts (steno-teles) commonly found in *Tubularia* spp. Intensive field studies are needed within the Eastport, Maine, Cobscook Bay area to obtain more information on the ecology of *C. salmonacea*. 
**Coryphella verrucosa** (M. Sars 1829)

Plate VII, Fig. 2

**Eolidia verrucosa** Sars, M. 1829. p.9 (Bergen, Norway)

**Eolis rufibranchialis** Johnston, 1832. p.428 (Berwick Bay, England)

**Eolidia embletoni** Johnston 1835. p.378 (Berwick Bay, England)

**Eolis diversa** Couthouy 1839. p.187 (Chelsea Beach, Massachusetts, U.S.A.)

**Eolidia diversa** (Couthouy). DeKay 1843. p.9

**Coryphella rufibranchialis** (Johnston). Gray, M. 1850. Vol. 4, p.109

**Eolis mananensis** Stimpson 1853. p.26 (Hake Bay, Grand Manan Is., Canada)

**Aeolis bostoniensis** 'Couthouy', Mørch, 1857. p.6 non-

**bostoniensis** Couthouy 1838; Lemche, 1941. p.28

**Aeolidia rufibranchialis** (Johnston) Dall, 1870. p.249

**Coryphella robusta** Trinchese 1874. p.523 (Port Leopold, Arctic)

**Coryphella verrucosa** (M. Sars). Friele & Hansen, 1876. p.75

**Aeolis bostoniensis** var. **approximans** Mørch 1877. p.437

[nomen nudum]

**Coryphella landsburgii** (A & H). Trinchese, 1881. p.98

[In synonymy.]

**Coryphella diversa** (Couthouy). Bergh, 1885. p.52
Coryphella salmonacea (Couthouy). Bergh, 1886. p.7; Odhner, 1939. p.54

Coryphella sp. Bergh 1900. p.32

Coryphella rufibranchialis var. chocolata Balch 1909. p.35

Coryphella rufibranchialis var. mananensis Balch 1909. p.35


Coryphella lineata (Lovén). Odhner, 1926. p.27 [In synonymy.]

Coryphella gracilis var. bostoniensis Lemche 1936. p.141

Coryphella borealis (Odhner). Lemche, 1936. p.141 [Identification in error.]

Coryphella verrucosa rufibranchialis (Johnston). Odhner, 1939. p.58

Coryphella verrucosa verrucosa (M. Sars). Odhner, 1939. p.58

Geographic Distribution

C. verrucosa has a boreal-arctic distribution: in the western Atlantic from southern New England (Clark, 1975), north through the Gulf of Maine (Johnson, 1915) to East and West Greenland; in the eastern Atlantic from Iceland, the Faroes, Spitzbergen, Kola Peninsula, Barents and Kara Seas, the entire Norwegian Coast, southwards along the western European coasts, and the Mediterranean Sea (Lemche, 1941a,b).
Also in the eastern Pacific from the Bering Sea (Nichols, 1900; Lemche, 1929) and in the western Pacific from the Seas of Japan (Volodchenko, 1955) and Okhotsk (Roginskaya, 1963).

Description

Adult length 20–35mm. Body translucent white, centrally opaque to pinkish white from mature gonad; cerata tan, maroon, or red-brown with conspicuous white tips. Body form elongate, narrow (taller than wide); evenly tapered to elongate, pointed tail. White pigment stripe centrally located on back, from pericardium to tip of tail, also on distal surfaces of oral tentacles and rhinophores.

Oral tentacles long, thin, evenly tapered to blunt point; insert posterior to anterior oral surface, generally longer than rhinophores. Rhinophores annulate to rugose, with thin gradual taper; moderately separated basally. Head small, narrower than foot, with oval subterminale mouth. Anterior foot auricles pointed, equal to half foot width; prominent groove producing anterior labium with medial oral notch; groove extends into foot auricles.

Cerata clustered (5–7 clusters in adults), inserted in diagonal rows on slightly expanded notum and back; notum absent between clusters. Ceratal shape short, rotund to moderately long and lanceolate; smallest occurring laterally, largest medially. Genital orifice below first ceratal cluster, slightly anterior to center. Penis tubular with con-
spicuously flared terminal disk, rim fluted. Anus always below third ceratal row of second cluster on right side (pleuroproctic); renal pore within interhepatic space.

Jaws oval, masticatory border prominent, with 3-4 rows of irregular, pointed denticles (Fig. 15). Rachidian teeth moderately wide, central cusp prominent, with 4-8 lateral denticles. Lateral teeth acutely triangular, medial edge with 7-12 sharp denticles; distal tip often curved outward (Fig. 16).

Egg mass thin, round, non-undulating spirals (Type B; Hurst, 1967) upon flat surfaces, evenly spaced loops around hydroid stalks. Stroma with several thousand singly encapsulated eggs, 85-100μm in diameter; development time 7-10 days at 13°C; larvae planktotrophic with spiralled, Type I shell (Thompson, 1961).

**Occurrences**

*Coryphella verrucosa* has been collected throughout the entire Gulf of Maine both intertidally and subtidally to depths of 33 meters. They are always associated with the dominant epifaunal hydroid species at depth and are restricted to hard, rocky, cobble substrates. Adults are sexually mature intertidally and shallow subtidally from late March through early June in southern New Hampshire and Massachusetts and into July in the Eastport, Maine area. Deep subtidally, the reproductive season extends well into late summer and early fall throughout the Gulf
of Maine. In the shallow subtidal areas of southern New Hampshire and Massachusetts, settlement occurs in July through early September on *Tubularia* spp. Juveniles continue to grow through the fall, winter and early spring by feeding predominately on thecate campanularid and sertularid hydroids but, if these are scarce, they will feed upon the athecate hydroids, *Hydractinia echinata* Fleming 1828 and *Clava leptostyla* Agassiz 1862 as well as the colonial ascidian, *Botryllus schlosseri* (Pallas 1766). In the Gulf of Maine, *C. verrucosa* has an annual life cycle and the settling data indicate a 6-8 week planktonic stage.

**Discussion**

*C. verrucosa* remains the most taxonomically confused coryphellid species in both the American and European literature. It is hoped this review will offer a reasonably definitive resolution to this reoccurring problem. *C. verrucosa* (M. Sars 1829) was initially described from specimens collected in Bergen, Norway. Johnston (1832) shortly thereafter described similar animals from Berwick Bay, England, using the name *Eolis rufibranchialis*, and later again (1835) under the taxon *Eolidia embletoni*. He later noted the similarities between the latter two and synonymized them (Johnston, 1838). Alder & Hancock (1855) subsequently designated *Eolis rufibranchialis* as the type species of *Coryphella* M. Gray 1850. The two names, *C. verrucosa* and *C. rufibranchialis* continued to be used and
confusion remained as to the validity of the two species (Bergh, 1878). Adding to the confusion were the morphologically similar species, Coryphella gracilis (Alder & Hancock 1843), C. pellucida (Alder & Hancock 1843), C. landsburgii (Alder & Hancock 1846) and C. smaragdina (Alder & Hancock 1851). This led Trinchese (1881) and Vayssière (1888) to group all the above species under the name C. landsburgii, while Bergh (1885, 1890) listed them as junior synonyms of C. rufibranchialis. Both these groupings were thought to be extreme by Eliot (1906) and he therefore rejected them except for the synonymy of C. gracilis and C. smaragdina (Eliot, 1906; 1910).

Balch (1909) described a new variety, C. rufibranchialis chocolata var. nov., based solely upon animals with dark, red-brown cerata. The new variety was justified because no intergrades could be found within the same population with a second variety with bright red cerata which he called C. rufibranchialis mananensis. He did however postulate that C. r. chocolata might be "a mere physiological phase". This fact was later proven by Morse (1969).

Løyning (1922) and Odhner (1922) simultaneously described the ceratal morphology and arrangement as being the only differences distinguishing C. verrucosa from C. rufibranchialis; cerata of C. verrucosa were shorter and more crowded (Odhner (1922) stated, cerata not arranged in clusters). However, Løyning (1922, 1927) stated he found
many intermediate stages between typical specimens of both forms and could find no demonstrable radular differences. He suggested using *C. rufibranchialis* as the senior synonym because it was the more common and better known name. Odhner (1926) however still listed the two forms as varieties of *C. rufibranchialis* and also included *C. lineata* (Lovén 1846) as a third variety. Lemche (1929) then followed suit and listed *C. lineata* as a junior synonym of *C. rufibranchialis*. However, Odhner (1939) later recognized *C. lineata* as a valid species after considering Løyning's (1927) findings but still recognized the two remaining forms as *C. verrucosa verrucosa* (with short, clavate cerata and restricted to northern Norway) and *C. verrucosa rufibranchialis* (with long, lanceolate cerata and a wide boreal-arctic distribution).

Lemche (1941b) has since synonymized all forms of this species under the name *C. verrucosa* according to the Rules of Nomenclature: Law of Priority, and proposed (Lemche, 1964) that the name *C. rufibranchialis* be rejected from the Official List. This proposal was accepted (Opinion 781. Bull. Zool. Nomencl. 23:104,1966). However, in the latest report on the British Opisthobranch Molluscs, Thompson & Brown (1976) still maintained the two varieties, *C. v. verrucosa* and *C. v. rufibranchialis* and added a third, *C. v. smaragdina* (Alder & Hancock 1851). The criteria separating them are ceratal color and shape. However, as noted above, they erroneously included *Coryphella pellucida* and *C.*
gracilis as synonyms of the variety C. v. verrucosa while C. smaragdina, if maintained as a variety at all, should be allied with C. gracilis and not C. verrucosa. I have examined a live specimen collected from the British Isles and identified as C. verrucosa (including fertile egg masses subsequently deposited in the laboratory) and have compared them to specimens along the New England coast which we have been designating C. verrucosa rufibranchialis (see Morse, 1969; Franz, 1970; 1975). There were no demonstrable morphological or embryological (including larval shell) differences between the two forms and I therefore agree with Lemche's (1964) synonymy.

Couthouy (1839) described Eolis diversa from Chelsea Beach, Massachusetts, U.S.A., which Bergh (1885, 1890) suggested be allied with C. salmonacea (Couthouy 1838). Balch (1908) however stated the two were not identical but the species C. diversa needed further elucidation. After reviewing Couthouy's description (including figures), many of A. E. Verrill's radular slides designated C. diversa, and the radular slide prepared from the specimen reported by Bush (1883) as C. diversa, it is my opinion that Couthouy's species, C. diversa is a junior synonym of C. verrucosa M. Sars 1829. The same is also true for C. mananensis (Stimpson 1853) which Gould & Binney (1870) synonymized with C. rufibranchialis but which Balch maintained as a variety while Verrill held it as a distinct species (see Balch, 1909. p.36).
Trinchese (1874) described *Coryphella robusta* from a British Museum specimen (collected from Port Leopold, Arctic) which Bergh (1885) suggested was synonymous with *C. rufibranchialis*. Farran (1909) reported and described specimens collected off the Irish Coast as *Coryphella gracilis*. However, from the radular descriptions given for both these two species, there can be little doubt that *C. robusta* is synonymous with *C. verrucosa* and that Farran misidentified specimens of *C. verrucosa* as *C. gracilis*.

The ecological parameters of *C. verrucosa* in New England compare well with the European data. In New England, *C. verrucosa* has been found feeding upon almost all of the European hydroid species listed as prey for this nudibranch (Bruce, Colman & Jones 1963; Thompson, 1964; and Thompson & Brown, 1976). The annual reproductive season of *C. verrucosa* is also similar on both sides of the Atlantic, except that it may be slightly delayed or extended by approximately a month on the eastern Atlantic coasts (Bruce, et al., 1963). The substrate type and depth distributions are again identical after noting the depth limitations imposed by the sampling method used (SCUBA).

**General Discussion**

Six species of *Coryphella* are found in the Gulf of Maine and comprise nearly 20% of the total number of New England nudibranch species. From the data summarized in Tables III-3-5, it can be seen that they geographically
coexist but, for the most part, are spatially and/or temporally separated. *C. nobilis* Verrill 1880 appears to be restricted to depths greater than 20 meters, and spawns annually in the late spring. *C. verrucosa* occurs at similar depths as *C. nobilis* and has a similar life cycle. Both species, especially *C. verrucosa*, are eurytrophic in their prey selection and because of this appear not to compete for food. Settlement for both species occurs when suitable hydroid prey is especially abundant (i.e. *Tubularia* spp.).

*C. salmonacea* has an annual life cycle but breeds during the winter. As adults, this species feeds upon ascidians and thus does not compete with its congeners for hydroid prey which is not as abundant during the winter months. The juveniles do feed upon hydroids during the late spring and summer months. However, competition is reduced because of the plentiful food supplies available. There are no larval settling requirements because this species has direct development.

*C. verrilli* has been found only from depths greater than 20 meters and only on soft, silty sand substrates. This nudibranch has only been found feeding upon the solitary hydroid *Corymorpha pendula* Agassiz 1862. It exhibits remarkably rapid growth rates and unlike any other reported coryphellid species, has multiple eggs per capsule. It also appears to have at least two generations per year. This reproductive strategy appears to be extremely well suited for a specialist feeding upon a seasonally unstable
food supply that also has a patchy distribution. *C. verrilli* fits well into "group 2" proposed by Miller (1962) and Thompson (1964) for hydroid feeding nudibranchs. The same is also true for *C. gracilis* which has two to three generations per year. This coryphellid appears to be stenotrophic by primarily being associated with *Eudendrium* spp. If this hydroid species becomes scarce however, adult nudibranchs are capable of maintaining themselves on a more eurytrophic diet. Unfortunately not enough is known about the larval settling requirements of this species to speculate further about its life cycle but there is no direct evidence of competition with its congeners.

*C. pellucida* also appears to be stenotrophic in its diet, being primarily associated with *Eudendrium* spp. and *Tubularia* spp. It has a definite annual life cycle and does not appear to compete with *C. gracilis* with which it shares similar food preferences. When these two species have been collected together, *C. pellucida* has always appeared in small numbers and their hydroid prey were always abundant. Unfortunately, the data are incomplete for *C. pellucida* during the winter months when *Eudendrium* is scarce. Like *C. gracilis*, *C. pellucida* also must become more eurytrophic in order to survive through the winter to reproduce in the spring. The prey data reported by Miller (1961) supports this hypothesis.

In summary, the majority of the six New England species of *Coryphella* appear to be either spatially or tem-
perally separated. When cooccurrence does occur, there is either an abundant supply of a limited number of preferred species available to support their coexistence or, when their preferred prey is limited, their diets are sufficiently eurytrophic to allow them to switch to a greater variety of less abundant prey species and thus minimize direct competition.

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by the S. S. "Huxley" during July and August, 1907.

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<table>
<thead>
<tr>
<th>CHARACTERS:</th>
<th>C. gracilis</th>
<th>C. verrucosa</th>
</tr>
</thead>
<tbody>
<tr>
<td>Size: sexual maturity</td>
<td>3-12mm</td>
<td>15mm</td>
</tr>
<tr>
<td>Rhinophores vs. Oral Tentacles (length)</td>
<td>equal or longer</td>
<td>equal or shorter</td>
</tr>
<tr>
<td>Foot auricles</td>
<td>&gt; foot width</td>
<td>half foot width</td>
</tr>
<tr>
<td>Notum</td>
<td>expanded, continuous</td>
<td>reduced, discontinuous</td>
</tr>
<tr>
<td>Ceratal insertion</td>
<td>on notum</td>
<td>on dorsum</td>
</tr>
<tr>
<td>Ceratal clusters</td>
<td>4-6</td>
<td>6-7</td>
</tr>
<tr>
<td>Anal position (second cluster)</td>
<td>first row</td>
<td>third row</td>
</tr>
<tr>
<td>Penis shape</td>
<td>conical</td>
<td>discoid</td>
</tr>
<tr>
<td>Radula: rows</td>
<td>10-16</td>
<td>13-20</td>
</tr>
<tr>
<td>rachidian teeth</td>
<td>broad; cusp long</td>
<td>narrow; cusp moderately short</td>
</tr>
<tr>
<td>lateral teeth</td>
<td>sickle-shaped, broad</td>
<td>acutely triangular</td>
</tr>
<tr>
<td>Egg mass morphology</td>
<td>undulating coil</td>
<td>smooth coil</td>
</tr>
</tbody>
</table>
Table III-2

Summary of A. E. Verrill's paratype material determined to be *Coryphella salmonacea*

<table>
<thead>
<tr>
<th>USNM#</th>
<th>Original Identification</th>
<th>Data on label</th>
<th>Radular slide #</th>
</tr>
</thead>
<tbody>
<tr>
<td>382223</td>
<td><em>Coryphella</em> (Cuthona)</td>
<td>Mass. Bay-off Salem (42°30'N;70°45'W) 4 Aug 1877; 45°-46°F; USS Speedwell; gravelly bottom</td>
<td>10139</td>
</tr>
<tr>
<td>382226</td>
<td><em>Coryphella</em> (Cuthona)</td>
<td>Off Kittery Point, Me. (43°50'N;70°40'W) 4 Sep 1874; 42°F; USS Bache; 51 fms; hard, sandy bottom</td>
<td>10144</td>
</tr>
<tr>
<td>382231</td>
<td><em>Coryphella</em> (Cuthona)</td>
<td>Off Chatham, Cape Cod, Mass. (41°35'N;60°35'W) Sep 1879; USS Speedwell; 34.5 fms.</td>
<td>10157</td>
</tr>
<tr>
<td>382242</td>
<td><em>Coryphella</em> (Cuthona)</td>
<td>Gulf of Maine (42°44'N;70°38'W) 19 Aug 1878; USS Speedwell; 35 fms.</td>
<td>10189</td>
</tr>
<tr>
<td>382247</td>
<td><em>Coryphella</em> (Cuthona)</td>
<td>Gulf of Maine (42°44'N;70°38'W) 19 Aug 1878; USS Speedwell</td>
<td>10196</td>
</tr>
<tr>
<td>382258</td>
<td><em>Coryphella</em> (Cuthona)</td>
<td>Casco Bay, Maine; 1873; U. S. Fish Commission</td>
<td>10214</td>
</tr>
<tr>
<td>382260</td>
<td><em>Coryphella</em> (Cuthona)</td>
<td>Off Boon, 2nd Light (43°05'N;70°11'W) 40°F; USS Bache; 38 fms; soft, mud bottom</td>
<td>10220</td>
</tr>
<tr>
<td>382310</td>
<td><em>Aeolis</em> sp.</td>
<td>Bay of Fundy; 1872; Determined by Nils Odhner to be <em>Coryphella stimpsoni</em></td>
<td>-----</td>
</tr>
<tr>
<td>382315</td>
<td><em>Coryphella</em> (Cuthona)</td>
<td>Off Cape Ann, Mass. (42°25'N;70°23'W) 2 Sep 1878; 54.5°F; USS Speedwell; 23 fms; stony bottom</td>
<td>-----</td>
</tr>
<tr>
<td>382349</td>
<td><em>Coryphella</em> (Cuthona)</td>
<td>Gulf of Maine; Station 167; 19 Aug 1879; USS Speedwell</td>
<td>10198</td>
</tr>
<tr>
<td>382352</td>
<td><em>Coryphella</em> (Cuthona)</td>
<td>Bay of Fundy; 1872; U. S. Fish Commission</td>
<td>-----</td>
</tr>
</tbody>
</table>
### Table III-3

**SUMMARY OF SEASONALITY DATA**

<table>
<thead>
<tr>
<th>Species</th>
<th>Jan</th>
<th>Feb</th>
<th>Mar</th>
<th>Apr</th>
<th>May</th>
<th>Jun</th>
<th>Jul</th>
<th>Aug</th>
<th>Sep</th>
<th>Oct</th>
<th>Nov</th>
<th>Dec</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>C. gracilis</em></td>
<td>---</td>
<td>A,2;*</td>
<td>A,1;*</td>
<td>J,1</td>
<td>J,1</td>
<td>---</td>
<td>J,2</td>
<td>A,J,2</td>
<td>A,3;*</td>
<td>A,3;*</td>
<td>A,2;*</td>
<td>---</td>
</tr>
<tr>
<td><em>C. nobilis</em>(1)</td>
<td>J,2</td>
<td>J,2</td>
<td>---</td>
<td>---</td>
<td>A,1</td>
<td>---</td>
<td>---</td>
<td>A,J,1;*</td>
<td>---</td>
<td>J,2</td>
<td>J,2</td>
<td>---</td>
</tr>
<tr>
<td><em>C. pellucida</em></td>
<td>---</td>
<td>J,1</td>
<td>A,1</td>
<td>A,1;*</td>
<td>A,1;*</td>
<td>A,1;*</td>
<td>J,1</td>
<td>J,1</td>
<td>J,1</td>
<td>J,1</td>
<td>J,1</td>
<td>---</td>
</tr>
<tr>
<td><em>C. salmonacea</em></td>
<td>A,3;*</td>
<td>A,2;*</td>
<td>A,1;*</td>
<td>A,1;*</td>
<td>---</td>
<td>A,1;*</td>
<td>J,1</td>
<td>J,2</td>
<td>A,J,2</td>
<td>A,2;*</td>
<td>A,2;*</td>
<td>A,3;*</td>
</tr>
<tr>
<td><em>C. verrilli</em>(2)</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>A,2;*</td>
<td>A,2;*</td>
<td>---</td>
<td>A,2;*</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td><em>C. verrucosa</em></td>
<td>J,2</td>
<td>J,2</td>
<td>A,3;*</td>
<td>A,3;*</td>
<td>A,3;*</td>
<td>A,3;*</td>
<td>J,2</td>
<td>J,2</td>
<td>J,2</td>
<td>J,2</td>
<td>J,2</td>
<td>J,2</td>
</tr>
</tbody>
</table>

A= Adult; J= Juvenile; *= Egg masses
1= rare; 2= common; 3= numerous

(1) Kuzirian (manuscript in press)
(2) Kuzirian (manuscript submitted)
### Table III-4

#### SUMMARY OF ECOLOGICAL PARAMETERS

<table>
<thead>
<tr>
<th>Species</th>
<th>Depths Collected (N.E.)</th>
<th>Max. Reported Depth</th>
<th>Substrate Type</th>
<th>Food Preferences (New England)</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. gracilis</td>
<td>0–33m</td>
<td>----</td>
<td>Hard</td>
<td>Eudendrium spp.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Halecium articulosem;  Clytia johnstoni</td>
</tr>
<tr>
<td>C. nobilis(1)</td>
<td>20+m</td>
<td>100m (Lemche, 1941)</td>
<td>Hard</td>
<td>Halecium articulosem;  Sertularia cupressina;  Tubularia spp.</td>
</tr>
<tr>
<td>C. pellucida</td>
<td>0–20m</td>
<td>120m (Odhner, 1907)</td>
<td>Hard</td>
<td>Eudendrium dispar</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Tubularia spectabilis;  T. crocea</td>
</tr>
<tr>
<td>C. salmonacea</td>
<td>0–20m</td>
<td>672m (Lemche, 1941)</td>
<td>Hard</td>
<td>Amaroucium constellatum</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Tubularia spp.;  Campanularid species</td>
</tr>
<tr>
<td>C. verrilli(2)</td>
<td>20–25m</td>
<td>292m (Verrill, 1882)</td>
<td>Soft</td>
<td>Corymormpha pendula</td>
</tr>
<tr>
<td>C. verrucosa</td>
<td>0–35m</td>
<td>450m (Odhner, 1907)</td>
<td>Hard</td>
<td>Tubularia spp.;  Clava leptostyla;  Obelia spp.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Hydractinia echinata;  Campanularia spp.;  Sertularia spp.;  Botryllus schlosseri</td>
</tr>
</tbody>
</table>

(1) Kuzirian (manuscript in press)
(2) Kuzirian (manuscript submitted)
**Table III-5**

**SUMMARY OF REPRODUCTIVE DATA**

<table>
<thead>
<tr>
<th>Species</th>
<th>Egg Mass Morph.*</th>
<th>Eggs/Capsule</th>
<th>Veliger Shell Type**</th>
<th>Development Type***</th>
<th>Egg Diameter</th>
<th>Egg Capsule Diameter (Length)</th>
<th>Development Times (Days/Temp.°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. gracilis</td>
<td>B</td>
<td>1</td>
<td>1</td>
<td>Planktonic</td>
<td>50-60(\mu)m</td>
<td>120(\mu)m</td>
<td>10-15/9-10°C</td>
</tr>
<tr>
<td>C. nobilis(1)</td>
<td>B</td>
<td>1</td>
<td>1</td>
<td>Planktonic</td>
<td>80(\mu)m</td>
<td>130(\mu)m</td>
<td>10-14/8-10°C</td>
</tr>
<tr>
<td>C. pellucida</td>
<td>B</td>
<td>1</td>
<td>1</td>
<td>Planktonic</td>
<td>70-80(\mu)m</td>
<td>135(\mu)m</td>
<td>12-14/8-10°C</td>
</tr>
<tr>
<td>C. salmonacea</td>
<td>B</td>
<td>1</td>
<td>1</td>
<td>Direct</td>
<td>250(\mu)m</td>
<td>400(\mu)m</td>
<td>45-55/4-6°C</td>
</tr>
<tr>
<td>C. verrilli(2)</td>
<td>A</td>
<td>30+</td>
<td>1</td>
<td>Planktonic</td>
<td>70-80(\mu)m</td>
<td>875(\mu)m</td>
<td>20-30/5-6°C</td>
</tr>
<tr>
<td>C. verrucosa</td>
<td>B</td>
<td>1</td>
<td>1</td>
<td>Planktonic</td>
<td>85-100(\mu)m</td>
<td>160(\mu)m</td>
<td>7-8/13°C</td>
</tr>
</tbody>
</table>

* Hurst, 1967. A= tall ribbon; B= cylindrical cord

** Thompson, 1961. Type 1= spiral (non-inflated)

*** Thompson, 1967.

(1) Kuzirian (manuscript in press)

(2) Kuzirian (manuscript submitted)
Plate V

Fig. 1. *Coryphella gracilis* (Alder & Hancock 1844): dorsal view of living animal (scale=0.1mm).

Fig. 2. *C. gracilis*: right lateral view of an anesthetized animal; arrow indicates anal position below first ceratal row of second cluster (scale=0.1mm).
Plate VI

Fig. 1. *Coryphella salmonacea* (Couthouy 1838): dorsal view of two living animals; animal in upper left collected Cobscook Bay, Maine; animal in lower right collected York, Maine (scale=5.0mm).

Fig. 2. *C. salmonacea*: ventral view of living animal illustrating trefoil head shape (scale=5.0mm).
Plate VII

Fig. 1. Coryphella pellucida (Alder & Hancock 1843): dorsal view of living animal; arrow indicates common stalk for ceratal insertion (scale=2.5mm).

Fig. 2. Coryphella verrucosa (M. Sars 1829): dorsal view of living animal (scale=2.5mm).
Fig. 9. *Coryphella gracilis* (Alder & Hancock 1844): one jaw plate with enlarged view of the masticatory border and its dentition (scales=0.1mm).

Fig. 10. *C. gracilis*: radular diagram illustrating one tooth row (scale=0.01mm).
Fig. 11. Coryphella pellucida (Alder & Hancock 1843): one jaw plate with enlarged view of masticatory border and its dentition (scales=0.05mm).

Fig. 12. C. pellucida: radular diagram of a partial tooth row (scale=0.01mm).
Fig. 13. Coryphella salmonacea (Couthouy 1838): one jaw plate with enlarged view of masticatory border and its dentition (scales=0.25mm).

Fig. 14. C. salmonacea: radular diagram of one tooth row; lateral teeth indicate range of variation (scales=0.05mm).
Fig. 15. *Coryphella verrucosa* (M. Sars 1829): one jaw plate with enlarged view of masticatory border and its dentition (scales=0.25mm).

Fig. 16. *C. verrucosa*: radular diagram of one tooth row (scale=0.01mm).
BILOGRAPHICAL DATA

Name: Alan Mitchell Kuzirian

Date of Birth: 6 October 1946

Place of Birth: Providence, Rhode Island

Secondary Education: Cumberland High School, Cumberland, Rhode Island; graduated 1964.

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J. Molluscan Studies (in press)

Positions held: University of New Hampshire:


Northeastern University: