THE TEUTHOID RADULA AS A TAXONOMIC CRITERION WITH SPECIFIC REFERENCE TO THE FAMILIES ARCHITEUTHIDAE AND OMMASTREPHIDAE (CEPHALOPODA: COLEOIDEA)

MARGUERITTE LUISE MARKS ALDRICH

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by

Marguerite Luise Marks Aldrich, A.B.

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ABSTRACT

A study of the radular morphology of Cephalopoda was undertaken to determine the feasibility of its use as a taxonomic character.

A search of the literature for illustrations of radular teeth of as many species as possible was made. Using available original material studies were also carried out using preparations of additional species. Where possible, comparisons were made based on both original preparations and information from the literature. In all, a total of 92 species representing 22 families were considered and are illustrated herein.

A comparison of the illustrations and radular ribbon preparations of these specimens indicated morphological differences of such a degree as to facilitate separation even to the species level.

The illustrations and radular ribbon preparations of members of the Family Architeuthidae show that both historical records and current specimens from Newfoundland waters exhibit similarities in the configuration of their radular teeth. There are, however, sufficient differences in the morphology of the teeth of individual specimens to cast serious doubt upon the designation of all five specimens as *Architeuthis dux*. Other families, genera, and indeed species within genera, can be separated on the basis of their radulae. Since this is true, the situation in the Architeuthidae becomes increasingly

difficult to interpret on the basis of their radulae and on the limited amount of material available.

The members of the Family Ommastrephidae show definite familial similarities in their radular teeth. The recorded differences in the morphology of these teeth, however, facilitate their separation into genera, but subspecies of the genus *Illex* cannot be so separated. The three subspecies can be separated on the basis of radular morphometry. Also, the radular apparatus of *Illex illecebrosus coindetii* is apparently to be added to the list of characters exhibiting sexual dimorphism in that form.

The evidence cannot support the view that the cephalopod radula is without function. As suggested by Bidder and others, the radula functions in teuthoid forms as an aid in swallowing. Such usage causes a wearing-away of the cusps of the teeth and occasional loss of teeth, necessitating their continual replacement at the most posterior, or growing, portion of the radular ribbon.

Because of the above described phenomenon, only teeth from certain rows (those retained within the radular sac) are of such a uniform configuration as to warrant their use in taxonomy.

"...whose teeth are spears and arrows,
and their tongue a sharp sword."

- Psalms. lvii. 4.

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INTRODUCTION

Mollusca is a phylum of metazoan animals comprising the classes Monoplacophora, Amphineura, Gastropoda, Scaphapoda, Pelecypoda (Bivalvia) and Cephalopoda. All these classes, excepting the Pelecypoda (Bivalvia), possess an anatomical structure in common. This anatomical structure is the radula. The radula may be defined as a band or ribbon studded with regularly arranged spines (Bartsch, 1934) or teeth.

Survey of Molluscan Radular Apparatus

The Monoplacophora are known from Cambrian and Devonian fossils and were "rediscovered" during 1957 in *Neopilina galatheae*, which has a radula with 11 longitudinal rows of teeth in a long, coiled radular sac (Wilmoth, 1967). There is no record of fossil radulae in this class.

In the Amphineura, (Order Polyplacophora, chitons) the radula exhibits many transverse rows of teeth. Each horizontal row is made up of 17 teeth and the number is constant throughout the group. Each row consists of three central teeth bordered on either side by lateral teeth, marginal teeth and marginal plates (Fretter, 1937). Smith (1960) described the teeth as being "horny, recurved denticles" and are "borne on a tough, flexible ribbon". The most prominent tooth is the "major lateral", which bears a varying number (1-4) cusps.

However, some Amphineurans may possess a radula which is greatly reduced (Yonge, 1960). These are the Aplacophorans, one member of which, *Chaetoderma* sp., possesses but a single radular tooth (Meglitsch, 1967). In whole families of this Order, the radula is absent (Yonge, 1960).

The Scaphopoda or tusk shells have a well developed radula (Wilmoth, 1967) which is of relatively enormous size when compared to the rest of the digestive system (Owen, 1966). The radula possesses five longitudinal rows of teeth (Ludbrook, 1960) or spines (Bartsch, 1934). Abbott (1954), in describing the two families of scaphopods, Dentaliidae and Siphonodentaliidae, makes mention of the central radular tooth as being of taxonomic importance. Although it is generally held that scaphopods resemble pelecypods and may have come from a primitive pelecypod stock, it must have occurred before the bivalve radula was lost (Meglitsch, 1967).

In the Gastropoda, the radula is an extremely variable structure. When present it may exist only in the form of isolated teeth or as a tooth-studded, flexible ribbon possessing up to 750,000 teeth, as in the genus *Umbrella* (Bartsch, 1934). The ribbon may vary in width and length, thereby altering the number of longitudinal and transverse rows of teeth. In the periwinkle *Littorina* spp. it is coiled and, if extended, equals a length several times that of the entire animal (Bartsch, 1934). Most certainly the gastropod radula is the best known as it has been a subject of interest since Aristotle, who, in 350 B.C. described snail radular apparatus, although Sollas (1907), refers to Swammerdam as "the discoverer of the radula" in the middle seventeenth century. The first illustrations of radular ribbons in the scientific literature were apparently those by Poli in 1791, of gastropods (Abbott, 1954). The gastropod radular apparatus will be discussed more fully later, primarily with respect to its use as a basis for classification.

There remains but to consider the cephalopod radular apparatus. Both octopod and decapod cephalopods, with certain exceptions, possess a radular apparatus which has been described as being associated with their predatory habits. Robson (1929a) distinguished the carnivorous nature of the cephalopod radular teeth from the herbivorous type characteristic of other classes of molluscs, the latter forms having a multicusped tooth configuration associated with rasping and grazing activities. Gabe and Prenant (1957) may be quoted as an example of many workers who contended that the configuration of the radular apparatus, with particular reference to the teeth, represented a more developed or highly evolved condition with respect to that of the decapods.

Description of Radular Apparatus

The terms "radula" and "odontophore" are used by various workers to indicate the structure in the buccal cavity of molluscs used in the feeding process. Henderson and Henderson's 1966 edition of Dictionary of Biological Terms, defines radula and odontophore as:

> "radula - A short and broad strip of membrane with longitudinal rows of chitinous teeth in the mouth of most gastropods.

odontophore - The tooth-bearing organ in molluscs, including the radula, radular sac, cartilage, and muscles."

Webster's Third New International Dictionary (1966) defines these terms in a slightly different manner:

"radula - A chitinous band in nearly all mollusks except bivalves that bears numerous usu. very minute teeth on its dorsal surface and slides backward and forward by special muscles over a more or less protrusible prominence on the floor of the mouth and serves to tear up the food and draw it into the mouth.

odontophore - A usu. more or less protrusible structure in the mouth of most mollusks except the bivalves that supports the radula."

While the latter group of definitions are more detailed, they are not completely accurate when applied to cephalopods. For purposes of greater clarity, I here refer to the entire structure (Plate 1, Figures 1 and 2, Plate 2, Figure 1, and Plate 6, Figure 2) as the radular apparatus. That portion of the radular apparatus which is thickened and bears the teeth is here referred to as the radular ribbon. The enlarged portion adjoining the anterior section of the ribbon and either entirely or partially covering the prominent elevation on the floor of the mouth, is here designated as the radular hood.

The mouth parts of cephalopods are located in a relatively large, bulbous, muscular structure called the buccal mass, which is surrounded by the brachial apparatus. When the buccal mass is removed and stripped of its accessory tissue, the dark, hard, mandibles (beak) are readily apparent.

When the beak is opened (Plate 3, Figures 1 and 2) the fleshy ligula or tongue is seen (Plate 5, Figure 1) and immediately behind it

Plate 1

Fig. 1. Top and side views of radular ribbon of *Oncomelania* sp. (Gastropoda); anterior end to right. (Drawing after Shrock and Twenhofel, 1953).

Fig. 2. Odontophore of *Moroteuthis robusta* (Dall) (Verrill, 1876). Lateral view (x3.75). (Drawing after Verrill, 1880).

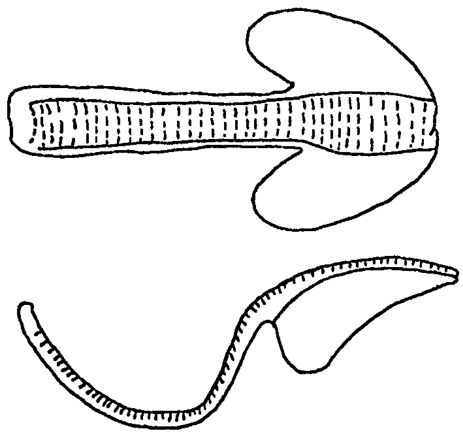

Fig. 1. Top and side views of radular ribbon of *Oncomelania* sp. (Gastropoda); anterior end to right. (After Shrock and Twenhofel, 1953)

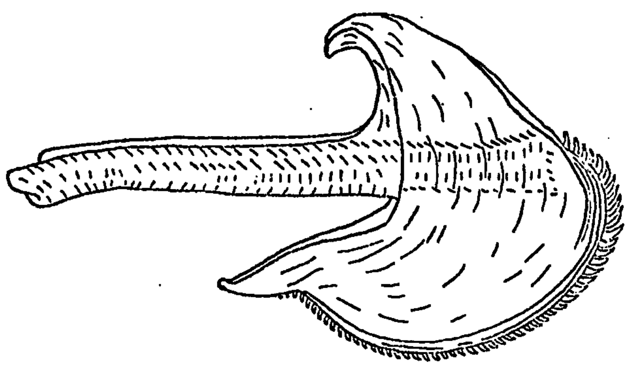

Fig. 2. Odontophore *Moroteuthis robusta* (Dall) (Verrill, 1876). (After Verrill, 1880)

Plate 2

Fig. 1. Photograph of entire radular apparatus of *Illex illecebrosus illecebrosus* (Lesueur, 1821). Original magnification x12.

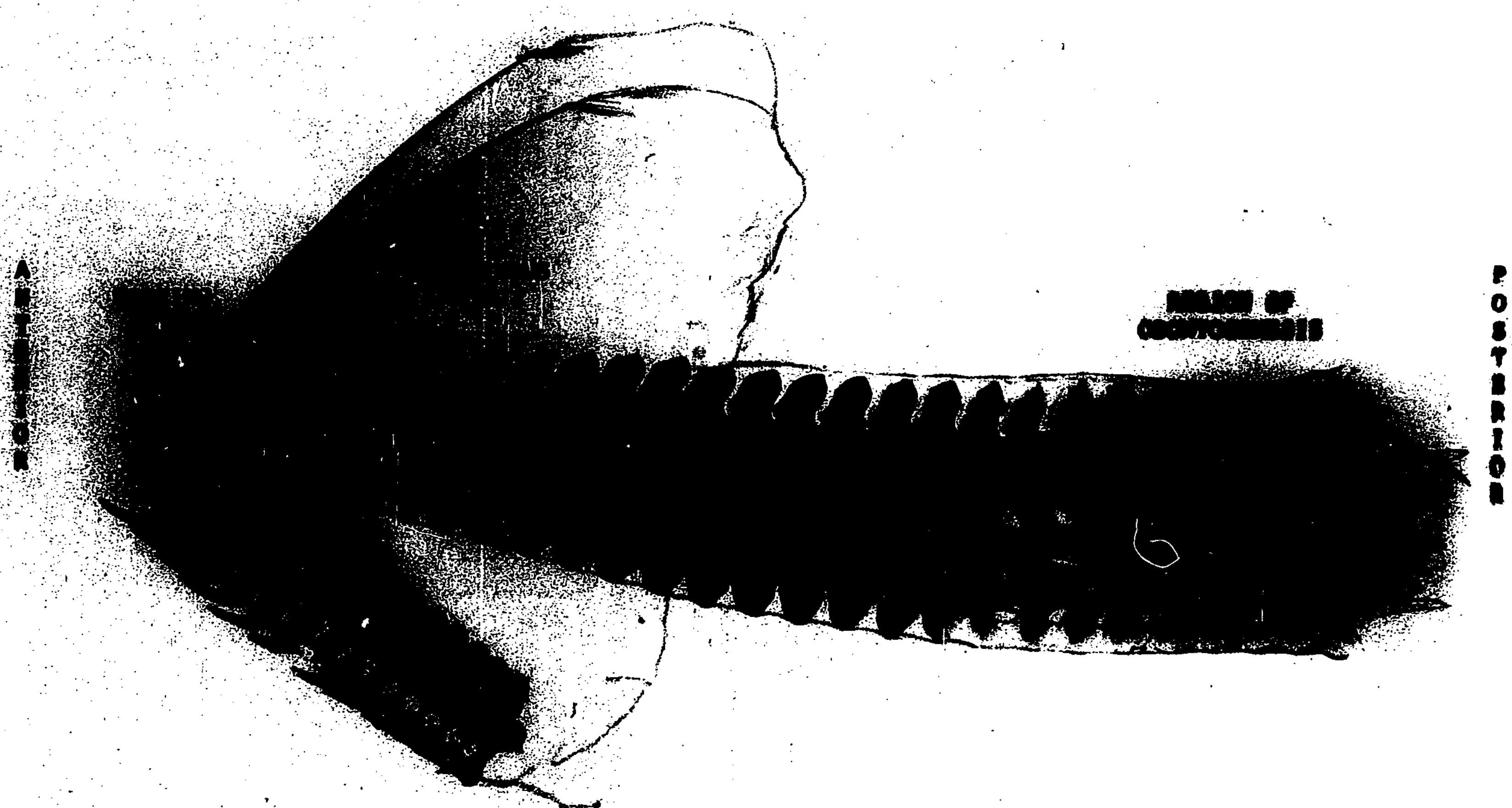

Fig. 1. Photograph of entire radula of *Illex illecebrosus illecebrosus*.

Plate 3

Fig. 1. Anterior view of buccal apparatus of Conche, White Bay, Newfoundland, specimen of *Architeuthis dux* Steenstrup, October 1964, showing mandibles and radular apparatus *in situ*. Photograph by H. James McCullough for Dr. F. A. Aldrich.

Fig. 2. Lateral view of buccal apparatus of Conche, White Bay, Newfoundland, specimen of *Architeuthis dux* Steenstrup, October 1964, showing mandibles and radular apparatus *in situ*. Photograph by H. James McCullough for Dr. F. A. Aldrich.

Fig. 1. *Architeuthis dux*
(Buccal apparatus, anterior view)

Fig. 2. *Architeuthis dux*
(Buccal apparatus, lateral view)

is the radular apparatus mounted upon the muscular prominence (Plate 4, Figure 1). In the gastropod, *Lymnea stagnalis*, the radular ribbon is firmly affixed to the underlying or subradular epithelium by radular chitin which the epithelium secretes (Carriker, 1947).[1] Surrounding the radular structures are lobes of tissue (buccal lobes), the superior surfaces of which are enlarged and covered with teeth of varying sizes, pointing posteriorly toward the esophagus. The radular teeth (Plate 5, Figure 2) are arranged so that they are also directed toward the esophagus. Only a portion of the radular ribbon is exposed (Plate 4, Figure 1) at any time. The rest is folded in upon itself, lengthwise, as it passes posteriad (Plate 4, Figure 2) and ventrad into a sac-like structure, the radular sac (Plate 6, Figure 1). One must agree with Bidder (1966) in her conclusion that "the texture of the fresh radula (not rigid) hardens on fixation".

The Teeth

The teeth of the cephalopod radular apparatus have been described by Bidder (1950) as being "delicate, flexible structures" which contrast strongly to the "hard dark jaws".

The terminology of radular teeth varies according to the author discussing them. As this thesis will demonstrate, there are different configurations of teeth comprising those of the horizontal rows. As will be later pointed out in more detail, there are normally seven

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[1]The only modern work on the microscopic anatomy of the secretory portions of the radular apparatus and its cytology is that of Gabe and Prenant (1957).

Plate 4

Fig. 1. Lateral view of radular apparatus of Architeuthid *in situ* with mandibles removed, showing the anterior curvature of the apparatus and including the attached chitinous hood. Specimen is that from Sweet Bay, Bonavista Bay, November 1965.

Fig. 2. Dorsal view of radular apparatus of Architeuthid *in situ*, showing posterior extensions or wings of the chitinous hood. The radular ribbon folds medially where it disappears into the radular sac. Specimen is that of Sweet Bay, Bonavista Bay, November 1965.

Fig. 1. Architeuthid radular apparatus
(Lateral view)

Fig. 2. Architeuthid radular apparatus
(Dorsal view)

Plate 5

Fig. 1. Dorso-frontal view of radular apparatus of Architeuthid *in situ*, with anteriorly placed ligula and the laterally located buccal lobes. Specimen is that of Sweet Bay, Bonavista Bay, November 1965.

Fig. 2. Ventro-frontal view of radular apparatus of Architeuthid *in situ*, showing oldest portion of the radular ribbon and teeth. Specimen is that of Sweet Bay, Bonavista Bay, November 1965.

Fig. 1. Architeuthid radula
(Dorso-frontal view)

Fig. 2. Architeuthid radula
(Ventro-frontal view)

Plate 6

Fig. 1. Dorsal view of that portion of radular apparatus which is normally enclosed in the radular sac. The specimen is the Architeuthid collected at Sweet Bay, Bonavista Bay, November 1965.

Fig. 2. Entire radular apparatus removed from the buccal cavity of Architeuthid, showing the chitinous hood and the curvative and medial folding of the radular ribbon. Specimen is that of Sweet Bay, Bonavista Bay, November 1965.

Fig. 1. Dorsal view of Architeuthid radular apparatus in opened radular sac.

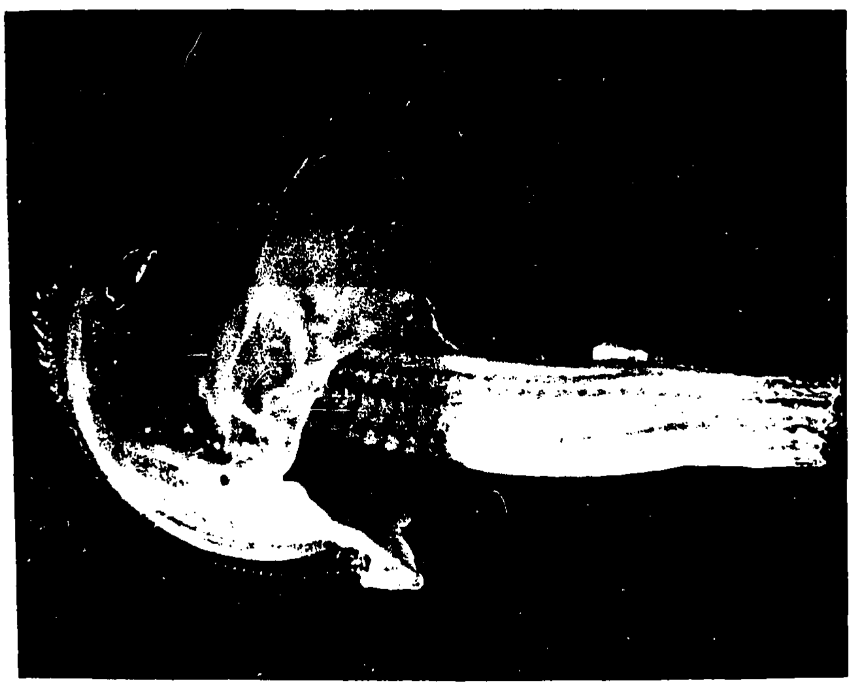


Fig. 2. Entire Architeuthid radular apparatus.

teeth in each horizontal row. They are arranged in such a fashion that there are three teeth to either side of a centrally located tooth. It is in the nomenclature of the several tooth types, according to their placement in relation to the central tooth, that different systems have been developed. Most frequently used systems are here compared in Table 1.

The list of systems here presented is not complete but is presented to show the range of difference in terminology employed and the basic similarity that exists in all the systems. In the following remarks, I have adopted the system used by Abbott (1954), namely, that of rachidian, lateral, inner and outer marginal teeth. The system is a simple one and I believe it to be correct in its coupling of the two outer-most rows as "marginals" (inner and outer) since these two teeth are, in fact, in close proximity and often overlap to a greater degree than do any of the others.

The teeth of different species and of different rows vary with respect to the number of cusps or projections. These have been designated by their position (external cusps or lateral cusps). The rachidian tooth in many species is tricusped. The median cusp has been called the mesocone, while those flanking it have been designated ectocones (Robson, 1925).

The cusps vary in height and have been described as being "worn" (implying damage) or "used", (Peile, 1937). Tryon (1879) in

Table 1. Comparison of systems of radular tooth nomenclature.

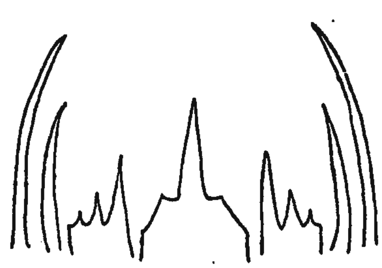
AUTHOR	ROWS						
	3	2	1	Central	1	2	3
Tryon (1879)	uncini	side	side	central	side	side	uncini
Verrill (1880)	outer	outer lateral	inner lateral	median	inner lateral	outer lateral	outer
Kirk (1888)	lateral	sublateral	submedian	median	submedian	sublateral	lateral
Sasaki (1929)	marginal	outer lateral	inner lateral	median	inner lateral	outer lateral	marginal
Robson (1929a)	3rd lateral	2nd lateral	1st lateral	rhachidian	1st lateral	2nd lateral	3rd lateral
Abbott (1954)	outer marginal	inner marginal	lateral	rachidian	lateral	inner marginal	outer marginal
Voss (1956)	3rd lateral	2nd lateral	1st lateral (or admedian)	rachidian (or median)	1st lateral (or admedian)	2nd lateral	3rd lateral

describing the radula of the cuttlefish *Sepia* sp. spoke of the continuous growth of the teeth which compensates for the loss of teeth by abrasion. Others wrote of the wearing away, through use, of the cusps. The older, "working teeth", of the radula of *Enoploteuthis anapsis* toward the tip of the radula are considerably more blunt than are the "young, unused teeth" which appear continuously from the radula sac (Roper, 1966). The most recent and valid work on the growth of the radular apparatus and the replacement of lost or worn teeth is that of Nixon (1968), on *Octopus vulgaris*.

One of the foremost workers on the cephalopod radular apparatus was G. C. Robson (1925, 1929a, 1929b, 1932). It was his contention that the Family Octopodidae was divisible into two groups on the basis of the structure of the radular rachidian tooth. He found that certain octopods have multicusped rachidian teeth, which exhibit a serial arrangement of ectocones (seriation) in successive sets of teeth, as the ectocones are located more externally. For a sequence of variation to be completed, as in the case of *Octopus vulgaris*, five rachidian teeth may be involved (Robson, 1925). He later was of the opinion that seriation changes with the age of the octopod (Robson, 1929a).

There is, therefore, considerable variation in tooth structure within the radular apparatus of the octopods. At any rate, Robson (1932) concluded that the cephalopod radula demonstrated two distinct "tendencies" in both the decapod and octopod groups. One of these he referred to as unicuspid or more or less homodont, quoting the sepioids and the genus *Argonauta*, as examples. In the Teuthidida, *Loligo* and *Ommastrephes*, and in the Octopoda the genus *Ocythoë*, as examples, he described the second "tendency" as one in which a heterodont condition prevailed, with the addition of extra cusps and clearly differentiated tooth-types. He asked the question as to which is the more primitive condition, i.e., the homodont or the heterodont, concluding that the homodont form represented the primitive condition in octopods and postulated the same to be true in decapods (Robson, 1929b). Earlier, Brock (1880) had held the counter view, that the sepioid radula represented a condition of advanced evolution, while Naef (1921) was of the opinion that the decapod radula was typical of the ancestral type, apparently failing to distinguish between degrees of development between the radular dentition of *Loligo* and *Sepia*.

Until the work of Lehmann (1967) no information was available on the radular teeth of fossil forms such as those of the Ammonoidea. The radular teeth of two specimens of the ammonoid *Eleganticeras elegantulum* (Text Figure 1), as illustrated by Lehmann (1967) show a distinctly multicuspidate condition of the rachidian and lateral teeth. This would appear



Text Figure 1. Radular teeth of fossil *Eleganticeras elegantulum* (Young and Bird). After Lehmann, 1967.

to favour the argument supporting the primitiveness of the heterodont condition as being the more primitive, although Robson (1932) was able to comment that simplicity of radular teeth need not obviate complexity or evolutionary advancement of a species as reflected in other body parts.

In addition to the longitudinal rows of teeth on the radular ribbon, there are non-cusped and non-toothlike marginal plates ("roundish scales" of Verrill, 1880) to the side of the outer marginal teeth. These are not consistently present.

Composition of Radula

With specific regard to the cephalopod radular apparatus, there seems to be no recent body of information concerning its chemical composition.

Radulae have been variously described as a "chitinous band on a cartilagenous odontophore" (Shrock and Twenhofel, 1953); a muscular tongue covered with a thin chitinous film (Akimushkin, 1963); a "chitinous ribbon" (Carriker, 1947); and as curved and chitinous (Roper, 1966). The teeth are most often described as being composed of conchiolin (Shrock and Twenhofel, 1953), or of chitin (Halstead, 1959, 1965; Akimushkin, 1963). Carriker (1947) described the teeth as "glass-like . . . denticles" and Sollas (1907) found them to contain silica salts, certain minerals (including iron) with a "chitinous basis". She is not the only one to report the presence of iron.

As reported by Silvernale (1965), Lowenstam of the California Institute of Technology discovered in 1963 that the teeth of unidentified chitons are composed of a "substance similar to dentin . . . coated with magnetic iron (black magnetite)", rendering them sufficiently hard to "cut limestone and scratch glass". Lowenstam went on to speculate that the iron is of dietary origin, derived from consumed algae.

Function of the Radular Apparatus

Wilmoth (1967) generalized that all radulate classes of mollusca utilize the radular apparatus in feeding activity. That this is true for some groups is certainly well established for both carnivorous and herbivorous species (Bartsch, 1934; Carriker, 1947; Owen, 1966). Specific functions have been described, namely, rasping (Owen, 1966, for Amphineura), rasping and food transfer to esophagus (Bartsch, 1934, for Scaphopoda), triturating and food transfer to esophagus (Owen, 1966, for Scaphopoda), masticating (Bartsch, 1934, Scaphopoda), rasping and triturating (Owen, 1966, for Gastropoda), and boring (Carriker, 1947, for Gastropoda).

In addition, gastropods of the Families Lamellareacea and Cypraeacea utilize the radular apparatus to penetrate the tunic of compound ascidians. In the opening thus made, the gastropod deposits egg capsules (Ankel, 1935; Fretter and Graham, 1964). Another example of specialized radular usage is that in the Family Conidae. The *Conus* spp. no longer possess a radular ribbon. Instead, they possess a sac-like structure wherein hollow, barbed, chitinous teeth are made and stored. Each tooth is used only once, in the manner of a poison-filled harpoon, to capture and paralyze prey (Halstead, 1959, 1965).

With respect to the Class Cephalopoda, the use of the radular apparatus is not as well understood as it is in other classes. Peile (1937) described its function in *Sepia officinalis* as "tearing flesh from prey held by the jaws and conveying the pieces to the oesophagus". The role he observed in *Octopus vulgaris* was "finishing the work, begun by the beaks, of carving crustaceans".

Stenzel (1964) ascribes no feeding function to the *Nautilus* radular apparatus. There appears to be little uniformity of opinion regarding the role of the radular apparatus of decapods in feeding activity. Yonge (1960) concluded that the radular apparatus was used as an aid in swallowing food bitten off by the jaws. This "cat tongue" usage is also ascribed to the radular apparatus of squid by Bidder (1950, 1966). She based her conclusions upon the condition of newly swallowed food in the stomach and on the speed with which it was swallowed, observing that no evidence of rasping could be ascertained as a meal was consumed in so short a period of time as to preclude this action of the radular apparatus. However, Akimushkin (1963) correlated the size of the radular apparatus with the size of food organisms, i.e., the greater the reduction of the radular apparatus, the smaller the size of the food organisms. If this is true, then it could be inferred from observations on the radular apparatus of the giant squids from Newfoundland waters, that the food organisms would be correspondingly small. The largest intact radular ribbon from this species is small in relation to the mantle length when compared with radular size and mantle length of other decapod species.

The clearest demonstration of the function of a cephalopod radula is that by Pilson and Taylor (1961). They demonstrated that the radulae of the octopods *Octopus bimaculoides* Pickford and McConnaughey and *O. bimaculatus* Verrill drill holes through the shells of a range of molluscan prey and permit the entry of paralyzing venom produced in the posterior pair of salivary glands.

Earlier, mention was made of Lowenstam's findings with respect to the presence of black magnetite or magnetic iron in the radular teeth of amphineurans (Silvernale, 1965). He is reported to postulate a navigational function to these teeth, in that the chitons are able to locate their rock-depression abodes with reference to magnetism. Indeed, if so, a unique role for teeth.

The Use of the Radular Apparatus in Molluscan Taxonomy

The radular apparatus has been used as a taxonomic aid in molluscan systematics for some time. Fisher (1880) introduced the term "glossophora", using it consistently in groups of different taxonomic rank to distinguish radula-bearing from non-radular-bearing (aglossa) forms. Von Zittel (1881) used the term Glossophora to include all members of the Polyplacophora (Class Amphineura), Scaphopoda and Gastropoda, whereas Lankester's (1883) use of this term included all molluscan classes with the exception of the Pelecypoda.

At one time the Amphineura were once grouped on the basis of radular configuration alone (Thiele, 1893, 1909-10, 1929), although current thinking tends to disregard this system (Smith, 1960).

The radular apparatus is of great significance in familial designation of gastropods (Abbott, 1954). The modified radular teeth of the Conidae is the basis upon which the Suborder Toxifera (Gray, 1853) was founded. Dentition formulae are important to the correct description and diagnoses of gastropods and in much the same manner, Robson (1929a) devised a system for the radular teeth of octopods (R = rachidian or "radial" tooth, A = symmetrical "denticles" or cusps, B = asymmetrical cusps, etc.)

Owens divided the Cephalopoda into two groups, based on the number of ctenidia, namely, the Dibranchiata and the Tetrabranchiata. Similarily, Schwarz erected two major groups, Ectocochlia and Endocochlia, basing these upon the location of the shell - inside or outside the body. Lehmann (1967) pointed out that Owen's system is not acceptable as it is based on structures that cannot be studied in fossil forms. No systematic treatment can be considered complete unless it incorporates the fossil forms studied by paleozoologists, which are definitely in the majority within the class.

Two specimens of the ammonoid, *Eleganticeras elegantulum* (Young and Bird) were made available to Lehmann (1967) and these both possessed radular ribbons with seven longitudinal rows of teeth. This is the first reference to fossil radular structures in the literature. It indicates that the Ammonoidea were not similar to the recent representatives of the Nautiloidea which possess 13 longitudinal rows of radular teeth. With respect to the radular apparatus, Lehmann concluded that the ammonoides are properly grouped with the Coleoidea, having seven longitudinal rows of radular teeth in common. In much the same way as Owens and Schwarz, Lehmann established two groups of cephalopods, the Lateradulata (Nautiloidea) and the Angusteradulata (Ammonoidea and Coleoidea).

Within the Suborder Incirrata (Octopoda) Naef (1922) established the Tribes Ctenoglossa (having multicuspidate rachidian and lateral teeth) and Heteroglossa (having multicuspidate rachidian teeth with the seriation mentioned earlier). Robson (1932) and Akimushkin (1963), both outstanding workers in the field of octopod biology, retained these distinctions, although the Suborders Cirrata and Incirrata have wide usage following their introduction by Grimpe (1917).

Robson (1929a) placed little importance on the seriation he described (1925) in species identification. He observed, however, that species "distinguished by other characteristics tend to have different types of seriation". He felt that the lateral teeth were of considerable taxonomic or diagnostic value (Robson, 1929a).

The "vampire squids", placed in the Order Vampyromorpha by Pickford (1949), were long considered to be octopods. Again, using the radular apparatus as the basis of his classification, Naef (1922) placed these forms in a unique group, the Odontoglossa.

It is evident that in the Class Cephalopoda the radular apparatus has been of considerable systematic importance, although little attention has been given to that of the decapods.

Several attempts have been made to set up criteria for taxonomic groupings in the Cephalopoda by using various structures, chiefly hard parts. Clarke (1962a),using the mandibles of representative species of 13 families of decapods, concluded that stable criteria exist whereby it is possible to identify beaks to family level. He found some instances of characteristics whereby he was able to distinguish between species but within the same family.

Earlier, Ishikawa (1924) showed that the statocysts of the Cephalopoda were of extremely important systematic significance and he urged that it be used as a criterion to determine the phylogenetic position of individual genera. Since the radular apparatus has been used in similar ways in other groups of molluscs, it was deemed advisable to undertake the present study with respect to a detailed examination of the radular teeth in as many forms as it was possible to obtain.

The purpose of this study is essentially threefold; (1) to study the general morphology of the Coleoid radular apparatus, (2) to examine the extent of variation within selected taxonomic groupings with respect to the morphology of the radular ribbon, and (3) to determine the role of the radular ribbons and teeth as taxonomic critera.

Synopsis of the Cephalopods examined for radular construction and configuration in this study

The synopsis which follows is the result of considerable effort taken to prepare as complete as possible a system of classification through major taxa and species, having sought out authorities and chronology at all levels. It was felt important to do this because synopses in the literature most often fail to take cognizance of the historical aspects of the development of systematic teuthology. It is recognized that several schemes of classification exist and the one adopted here proved to be workable and reflects the relationships between the different taxa concerned. In addition to original papers for individual taxa, references used in the preparation of this synopsis were basically Férussac, 1839; Pfeffer, 1912; Naef, 1923; Clarke, 1966; Robson, 1929-1932; Sweet, 1964; Teichert & Moore, 1964; and numerous publications by G. L. Voss. Special mention should be made in acknowledging the co-operation of Mr. C. C. Lu, of the staff of the Marine Sciences Research Laboratory, in the preparation of various areas of this synopsis. Especially to be acknowledged is his cheerful assistance and the opportunity to gain access to his extensive library of reprints pertaining to the literature of cephalopods.

Phylum Mollusca
Class Cephalopoda Cuvier, 1797
Subclass Nautiloidea Agassiz, 1847
Order Nautilida Agassiz, 1847
Family Nautilidae de Blainville, 1825
Genus *Nautilus* Linné, 1758
Nautilus pompilius de Montfort, 1808

Subclass Coleoidea Bather, 1888[1]
Order Sepioidea Naef, 1923
Family Sepiidae Leach, 1817
Genus *Sepia* Linné, 1758
Sepia officinalis Linné, 1758
Sepia orbigniana Férussac, 1826
Sepia elegans de Blainville, 1827
Sepia lorigera Wülker, 1910
Sepia longipes Sasaki, 1914

Family Sepiolidae Leach, 1817
Subfamily Rossiinae Hoyle, 1904
Genus *Rossia* Owen, 1828
Rossia macrosoma d'Orbigny, 1839
Rossia sublevis Verrill, 1878
Rossia (Semirossia) tenera (Verrill, 1880)
Rossia caroli Joubin, 1902
Rossia mollicella Sasaki, 1920
Rossia (Austrorossia) antillensis Voss, 1955
Rossia sp.

Subfamily Sepiolinae Hoyle, 1904
Genus *Sepiola* Leach, 1817
Sepiola atlantica d'Orbigny, 1839
Sepiola (= Sepietta) oweniana d'Orbigny, 1839

Order Teuthidida Naef, 1916
Suborder Myopsida d'Orbigny, 1839
Family Loliginidae d'Orbigny, 1839
Genus *Loligo* Schneider, 1784
Loligo vulgaris Lamarck, 1799
Loligo pealei Lesueur, 1821
Loligo forbesi Steenstrup, 1856
Loligo japonica (Steenstrup, 1885)
Loligo edulis Hoyle, 1885
Loligo etheridgei Berry, 1918

[1] Includes Decapoda Leach, 1818.

Genus *Doryteuthis* Naef, 1912
Doryteuthis singhalensis (Ortmann, 1891)
Doryteuthis pickfordae Adam, 1954
Doryteuthis sibogae Adam, 1954
Genus *Lolliguncula* Steenstrup, 1881
Lolliguncula brevis (de Blainville, 1823)
Genus *Sepioteuthis* de Blainville, 1824
Sepioteuthis lessoniana Férussac, 1826
Genus *Alloteuthis* Wülker, 1920
Alloteuthis media (Linné, 1758)
Genus *Uroteuthis* Rehder, 1945
Uroteuthis bartschi Rehder, 1945
Genus *Loliolus* Steenstrup, 1856
Loliolus investigatoris Goodrich, 1896

Suborder Oegopsida d'Orbigny, 1839
Family Enoploteuthidae Pfeffer, 1900
Subfamily Enoploteuthinae Pfeffer, 1900
Genus *Enoploteuthis* d'Orbigny, 1839
Enoploteuthis leptura (Leach, 1817)
Enoploteuthis anapsis Roper, 1964
Genus *Abralia* Gray, 1849
Abralia veranyi (Rüppell, 1844)
Abralia multihamata Sasaki, 1929
Genus *Abraliopsis* Joubin, 1896
Abraliopsis hoylei (Pfeffer, 1884)
Abraliopsis gilchristi (Robson, 1924)

Subfamily Pyroteuthinae Pfeffer, 1900
Genus *Pterygioteuthis* Fischer, 1896
Pterygioteuthis giardii Fischer, 1896

Family Onychoteuthidae Gray, 1849
Genus *Onychoteuthis* Lichtenstein, 1818
Onychoteuthis banksi (Leach, 1817)
Genus *Ancistroteuthis* Gray, 1849
Ancistroteuthis lichtensteinii (d'Orbigny, 1839)
Genus *Moroteuthis* Verrill, 1881
Moroteuthis robusta (Dall) (Verrill, 1876)
Moroteuthis lönnbergii Ishikawa & Wakiya, 1914

Family Gonatidae Hoyle, 1886
Genus *Gonatus* Gray, 1849
Gonatus fabricii (Lichtenstein, 1818)
Gonatus magister Berry, 1913
Gonatus anonychus Pearcy & Voss, 1963

Family Pholidoteuthidae Adam, 1950
  Genus *Pholidoteuthis* Adam, 1950
    Pholidoteuthis adami Voss, 1956

Family Architeuthidae Pfeffer, 1900
  Genus *Architeuthis* Steenstrup, 1857
    Architeuthis dux Steenstrup, 1857
    Architeuthis harveyi Verrill, 1875
    Architeuthis longimanus Kirk, 1888
    Architeuthis sp. (of Mitsukuri & Ikeda, 1895)
    Architeuthis physeteris (Joubin, 1899)
    Architeuthis clarkei Robson, 1933
    Architeuthis sp. (of Frost, 1934)
    Architeuthis sp. (of Frost, 1935)

Family Histioteuthidae Verrill, 1881
  Genus *Histioteuthis* d'Orbigny, 1839
    Histioteuthis bonelli (Férussac, 1835)
    Histioteuthis collinsii (Verrill, 1879)
  Genus *Calliteuthis* Verrill, 1880
    Calliteuthis reversa Verrill, 1880
    Calliteuthis dofleini (Pfeffer, 1912)
    Calliteuthis elongata Voss & Voss, 1962
    Calliteuthis corona Voss & Voss, 1962
    Calliteuthis (= *Meleagroteuthis*) *hoylei* Pfeffer, 1908
    Calliteuthis (= *Stigmatoteuthis*) sp.

Family Bathyteuthidae Pfeffer, 1912
  Genus *Bathyteuthis* Hoyle, 1885
    Bathyteuthis bacidifera Roper, 1968
    Bathyteuthis berryi Roper, 1968
    Bathyteuthis sp.

Family Batoteuthidae Young & Roper, 1968
  Genus *Batoteuthis* Young & Roper, 1968
    Batoteuthis scolops Young & Roper, 1968

Family Brachioteuthidae Verrill, 1881
  Genus *Brachioteuthis* Verrill, 1881
    Brachioteuthis beanii Verrill, 1881

Family Ommastrephidae Gill, 1871
 Subfamily Illicinae Posselt, 1890
  Genus *Illex* Steenstrup, 1880
    Illex illecebrosus illecebrosus (Lesueur, 1821)
    Illex illecebrosus coindetii (Verany, 1837)
    Illex illecebrosus argentinus de Castellanos, 1960
  Genus *Todaropsis* Girard, 1889
    Todaropsis eblanae (Ball, 1841)

Subfamily Todarodinae Pfeffer, 1912
Genus *Todarodes* Steenstrup, 1880
Todarodes sagittatus (Lamarck, 1799)

Subfamily Ommastrephinae Carus, 1890
Genus *Ommastrephes* d'Orbigny, 1839
Ommastrephes bartrami (Lesueur, 1821)
Ommastrephes pteropus (Steenstrup, 1855)
Genus *Ornithoteuthis* Okada, 1927
Ornithoteuthis antillarum Adam, 1957

Family Thysanoteuthidae Keferstein, 1866
Genus *Thysanoteuthis* Troschel, 1857
Thysanoteuthis rhombus Troschel, 1857

Family Chiroteuthidae Gray, 1849
Subfamily Chiroteuthinae Chun, 1910
Genus *Chiroteuthis* d'Orbigny, 1839
Chiroteuthis veranyi (Férussac, 1835)
Chiroteuthis capensis Voss, 1967
Genus *Valbyteuthis* Joubin, 1931
Valbyteuthis danae Joubin, 1931

Family Mastigoteuthidae Chun, 1910
Subfamily Mastigoteuthinae Chun, 1910
Genus *Mastigoteuthis* Verrill, 1881
Mastigoteuthis cordiformis Chun, 1908

Family Promachoteuthidae Naef, 1912
Genus *Promachoteuthis* Hoyle, 1885
Promachoteuthis sp.

Family Cranchiidae Prosch, 1847
Subfamily Cranchiinae Pfeffer, 1912
Genus *Pyrgopsis* de Rochebrune, 1884
Pyrgopsis pacificus Issel, 1908
Genus *Verrilliteuthis* Steenstrup, 1856
Verrilliteuthis hyperborea (Steenstrup, 1861)
Subfamily Taoniinae Pfeffer, 1912
Genus *Phasmatopsis* de Rochebrune, 1884
Phasmatopsis cymoctypus de Rochebrune, 1884
Genus *Megalocranchia* Pfeffer, 1884
Megalocranchia megalops australis Voss, 1967

Order Octopoda Leach, 1817
Suborder Incirrata Grimpe, 1917
Family Octopodidae d'Orbigny, 1838
Subfamily Octopodinae Grimpe, 1921
Genus *Octopus* Cuvier, 1797
Octopus vulgaris Lamarck, 1798
Octopus bairdii Verrill, 1880
Octopus (*Polypus*) *fujitai* (Sasaki, 1929)
Octopus salutii Verany, 1839
Genus *Pteroctopus* Fischer, 1882
Pteroctopus tetrachirrhus (Delle Chiaje, 1830)

Subfamily Bathypolypodinae Robson, 1931
Genus *Bathypolypus* Grimpe, 1921
Bathypolypus sponsalis Robson, 1921

Family Argonautidae Cantraine, 1841
Genus *Argonauta* Linné, 1756
Argonauta argo Linné, 1756
Argonauta hians Solander, 1786

Family Ocythoidae Gray, 1849
Genus *Ocythoë* Rafinesque, 1814
Ocythoë tuberculata Rafinesque, 1814

MATERIALS AND METHODS

An effort was made to determine the radular morphology of as many species of decapod Coleoids as possible. Emphasis was placed on teuthoid species, and octopods were included only as a basis of comparison.

Where specimens were not available, primary and secondary sources in the literature were consulted and radular illustrations therein used as a basis for comparison. In many instances neither size nor scale was indicated in the original. For this reason, the drawings have been reproduced either in the original size, enlarged or reduced as fitted the circumstances. Reproduction of the drawings was carried out as accurately as possible using a table-mounted Optiskop TYP 62 1000, equipped with an Optiscop lens 1:4/175, an Optilux lens 1:25/100, and an Extension Tube. It is manufactured by the Optelma Grafica ag., Basel, Switzerland.

All photomicrographs were taken by the author using ADOX KB 14, 35 mm, 20 ASA film. The photomicrographic facilities used were those at the Marine Sciences Research Laboratory, a Nikon Microflex Photomicroscope, Model AFM. The film was developed and printed by Mrs. K. Yorke of the Marine Sciences Research Laboratory. Additional photographs of the radula and buccal mass of *Architeuthis* were taken, developed and printed by Mrs. Yorke, following the several stages of dissection by the author. The two photographs of the *Architeuthis* from Conche, White Bay (1964) were taken by Mr. H. James McCullough for Dr. F. A. Aldrich at the time of original examination.

All measurements are expressed in millimetres and are defined as follows:

Mantle Length

(ML) = the dorsal length of the mantle from the anterior margin to the posterior end. (Voss, 1956; Haefner, 1964)

Radular Length

(RL) = the total length of the radular ribbon from its growing edge, normally enclosed in the radular sac, to the base of the last row or partial row of teeth on the oldest or most anterior portion.

Radular Width

(RW) = the greatest width of the radular ribbon, at the growing edge, which extends slightly beyond the marginal teeth or marginal plates, where the latter are present.

Tooth Width

(TW) = the width of the middle or rachidian tooth, immediately below the lateral cusps or ectocones. Where lateral cusps or ectocones are not present, the widest portion of the base of the rachidian tooth above the radular ribbon may be used.

All measurements were made using either a standard millimetre rule or a standard calibrated occular micrometer, depending on the size of the material examined.

The original material for this study was made available from several sources. The sources and specimens are as follows:

1. MSRL/MUN Collections

Sepia elegans	(Courtesy of Dr. G. L. Voss, Institute of Marine Science, University of Miami)
Rossia sublevis	As above
Rossia sp.	As above
Rossia sp. larva	(Courtesy of Mr. N. J. Humby, Summerville, Bonavista Bay)*
Loligo pealei	
Lolliguncula brevis	(Courtesy of Dr. F. C. Daiber and Mr. R. W. Smith, University of Delaware, Marine Laboratories, Lewes, Delaware)
Abralia veranyi	(Courtesy of Dr. G. L. Voss , Institute of Marine Science, University of Miami)
Architeuthis dux	
Illex illecebrosus illecebrosus	
Illex illecebrosus coindetii	(Courtesy of Dr. G. L. Voss, Institute of Marine Science, University of Miami)
Illex illecebrosus argentinus	(Courtesy of Dr. Zulma J. A. de Castellanos, Museo de La Plata, La Plata, Argentina)
Onychoteuthis banksi	(Courtesy of Dr. G. L. Voss, Institute of Marine Science, University of Miami)

2. Dr. Katharina Mangold, Maître de Recherche, Laboratoire Arago, Banyuls-sur-Mer, France

   Sepia officinalis

   Sepietta oweniana = *Sepiola oweniana*

*As reported by Aldrich & Lu (1968a)

Rossia macrosoma

R. caroli

Illex illecebrosus coindetii

Todaropsis eblanae

Todarodes sagittatus

Octopus salutii

Pteroctopus tetracirrhus

Bathypolypus sponsalis

3. Dr. Clyde Roper, Supervisor, Division of Mollusks, U.S. National Museum, Smithsonian Institution, Washington, D.C.

Bathyteuthis sp.

The removal of the radula from the buccal cavity posed a problem. Dissection proved to be an unsatisfactory method as the radular apparatus adhered firmly to the underlying tissue and muscles, damaging extensively the teeth and the radular ribbon. It was found that immersion of the entire buccal mass in a 10 per cent solution of sodium hydroxide, for a period of 12-24 hours, softened and destroyed the tissues of the buccal mass, thereby greatly facilitating the removal of the radular apparatus intact from its position in the buccal cavity.

Upon the removal of the radular apparatus, it was thoroughly rinsed with tap water and then stored in 70 per cent ethyl alcohol until mounting. Before mounting,the radular apparatus was again washed in tap water to remove debris (fish scales, small sand grains, and bits of unidentifiable material) from between the longitudinal rows of teeth and the teeth themselves. The chitinous hood was trimmed from the radular ribbon by means of a micro dissecting scalpel. Further cleaning of the radular teeth was carried out by means of needles made from insect pins set into melted glass tubing and a fine water-colour paint brush, trimmed to a shorter length to make it less flexible.

The ventral portion of the radular ribbon was gently scraped with the micro dissecting scalpel in order to remove as much of the adhering tissue as possible. If this were not done, as it was not in a trial run of the technique, the adhering tissue would stain and render the radular ribbon opaque, thereby obscuring the details of the radular teeth.

Once trimmed and cleaned, the radular ribbon was mounted. The use of Turtox CMC-S*, Non-resinous Stain Mountant proved to be invaluable. I must here thank Dr. D. H. Steele for suggesting this material. This medium made possible the staining and mounting of the radular ribbon directly from either water or alcohol, without the dehydrating, staining, and clearing usually associated with histological technique. A quantity of the CMC-S, sufficient to cover the specimen and the area of a 22 mm x 22 mm, no. 1, cover glass, was placed on the slide. The specimen was then placed in the stain-mountant, oriented, flattened, and a cover glass placed on the specimen.

The CMC-S contains acid fuchsin which stains the cytoplasmic portion of the cellular components adhering to the radular ribbon, newly formed teeth, and bases of the older teeth. The cusps of the older teeth do not stain but remain transparent and "glassy" in appearance.

*Available from General Biological Supply House, Inc., 8200 South Hoyne Avenue, Chicago, Illinois 60620, U.S.A.

If at any time the specimen needed to be removed from the slide for re-positioning or the need to replace a cracked cover glass, etc., it could be done readily by soaking the slide in tap water. The water dissolves the CMC-S, leaving the specimen freely accessible and workable. The intensity of the stain is in no way diminished upon such treatment. By using CMC-S in conjunction with Turtox CMC-10 Non-resinous Transparent Mounting Medium, the degree of staining could be controlled. Both CMC-S and CMC-10 are mutually miscible and soluble in water and alcohol.

The radular apparatus of the Architeuthids proved to be difficult to handle. The large size and thickness of the radular ribbons were not the only sources of difficulty, but also their extreme brittleness. Having been stored in alcohol for a period of four or five years, the radular ribbons retained their natural curvature. Measurements and examination of teeth required that the radular ribbons be mounted, after the prerequisite cleaning and trimming. A radular ribbon was then oriented lengthwise on a plain glass slide (25 mm x 75 mm). In order to straighten and hold the radular ribbon in place, it was tied to the slide with nylon monofilament "Invisible Sewing Thread". The thickness of the radular ribbon necessitated the use of supports to contain the mounting medium and hold the cover glass, which was a second plain glass slide (25 mm x 75 mm). To do this a rectangular "crib" of FISHERbrand capillary glass tubing (I.D. 1.1-1.2 mm) was used. The tubing was secured to the four margins of the slide by a small amount of either CMC-S or CMC-10, and held in place until firmly set. The mounting medium was then poured into this enclosure covering the radular ribbon and a cover glass slide placed upon the preparation. The thickness of the preparation necessitated the use of a vacuum oven to remove trapped air, and I wish to thank Dr. G. I. McT. Cowan for his help with the techniques of this latter operation.

In all, a total of 20 specimens of *Illex illecebrosus illecebrosus* and 21 specimens of *I. i. coindetii* were examined. In each specimen, as in the other genera examined, the radular length was ascertained (in millimetres), along with determinations of the mantle length, sex, the buccal mass diameter, the greatest and smallest width of the radular ribbon, plus the number of longitudinal and horizontal rows of teeth on the radular ribbon. For specimens of the three subspecies of *I. illecebrosus*, three individuals were found to be of approximately the same mantle length (160-163 mm) and of the same sex (male). For these specimens, measurements were made of the width of the rachidian teeth (in millimetres), the height deemed to be too variable in as much as abundant evidence of wear or mesocone damage was prevalent. Such measurements were taken using an ocular micrometer.

Indices of radular length were then computed against mantle length for these three individuals.

In all instances, the number of specimens in all other families is indicated in the appropriate portions of the thesis.

The radular ribbons of the genus *Architeuthis* that were available were studied in similar fashion, in that the width of all of the rachidian teeth present were measured. Since only two of the five specimens of *Architeuthis* proved to possess complete radular ribbons it was deemed inadvisable to attempt to compute radular indices, although the information (i.e., data) will be presented here later.

RESULTS

In lieu of actual material, it was possible to find radular illustrations of representative genera and species of 22 families of cephalopods, from various sources in the literature. These are reproduced in Plates 7 through 49. I was able to examine the actual radular ribbons and teeth of 80 specimens representative of 15 genera and eight families. Photographs of radular teeth of representatives of these 15 genera augment the material from the literature sources and are to be found on the plates of the appropriate families.

All of the families represented, with two exceptions occurring in the families Gonatidae (Hoyle, 1886) and Chiroteuthidae (Adam, 1952), exhibit seven longitudinal rows of teeth. Both of the exceptions have only five such rows.

Family Nautilidae

The only living tetrabranch, *Nautilus*, possesses a radula of the usual seven longitudinal rows of teeth, plus well developed marginal plates. There is a unicuspid rachidian (median) tooth, the same condition with respect to cusps being exhibited by both the lateral and inner marginal teeth. The marginal teeth are sharply recurved, directed medially, posteriorly and dorsally, the outer curved surface directed toward the midline and overlaps adjacent inner marginal teeth (Plate 7, Figure 1).

Plate 7

Family Nautilidae

Fig. 1. Single row of radular teeth of *Nautilus pompilius* Linné, 1758. (Drawing after Naef, 1923)

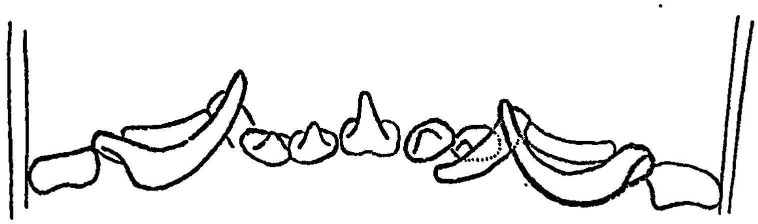


Fig. 1. *Nautilus pompilius* Linné, 1758.
(After Naef, 1923)

Family Sepiidae

In the Family Sepiidae, two species of the genus *Sepia*, *S. officinalis* and *S. elegans*, were available for examination (Plate 8, Figures 1 and 2). The data on these specimens are presented in Table 2.

Table 2. Mantle length, sex, buccal and radular data for representatives of Family Sepiidae.

Species	Mantle Length (mm)	Sex	Buccal Mass Diam. (mm)	Radula Length (mm)	Radula Max. Width (mm)	Radula Min. Width (mm)	Teeth No. of Horiz. Rows	Teeth No. of Longit. Rows
S. officinalis	135	F.	18	12.9	3.2	3.2	53	7
S. elegans	70	F.	8	6.5	1.6	1.05	49	7

In Plate 8, Figure 1, is presented a photograph of a portion of the radular ribbon of the cuttlefish *Sepia officinalis* described in Table 2. The dentition agrees fairly well with the drawing from Naef (1923) as presented in Plate 9, Figure 1, to be discussed shortly.

In Plate 8, Figure 2, is presented a portion of the radular ribbon of *Sepia elegans*. As can be seen by comparing Figures 1 and 2 (Plate 8) and the sepioids figures in Plate 9, *S. elegans* is characterized by the possession of moderately developed marginal plates and extremely long cusps on a broad-based rachidian tooth. As in other species of the genus represented, *S. elegans* possesses lateral teeth of a length equal, or nearly equal, to that of the rachidian teeth.

As noted earlier, a representation of the radular ribbon of *S. officinalis* was available in the literature (Naef, 1923). This illustration (Plate 9, Figure 1), shows seven teeth, all unicuspid, long, and of almost equal length and moderately acute. The marginals are the longest and they curve medially to a slight extent and then upward.

Three additional species are depicted in Plate 9. These are *Sepia orbigniana* (after Naef, 1923) (Figure 2), *S. longipes* (after Sasaki, 1929) (Figure 3) and *S. lorigera* (after Sasaki, 1929) (Figure 4). The radular teeth represented in these sources differ markedly, mainly in the development of the cusps of the rachidian, lateral and inner marginal teeth, and also in the size and extent of their bases. Three factors in common are the equality, or near equality, of length of the laterals and rachidian teeth, the unicuspid condition, and the elongated recurved configuration of the marginal teeth, which are similar to that characteristic of *S. officinalis* (Plate 9, Figure 1).

The irregular tooth displacement seen in Plate 8, Figure 2, is due to damage in handling and is not natural.

<u>Family Sepiolidae</u>

Genus *Rossia*

Specimens of three species of the genus *Rossia* were available

Plate 8

Family Sepiidae

Fig. 1. Photograph of radular teeth of *Sepia officinalis* Linné, 1758.

Fig. 2. Photograph of radular teeth of *Sepia elegans* de Blainville, 1827.

Fig. 1. *Sepia officinalis* Linné, 1758.

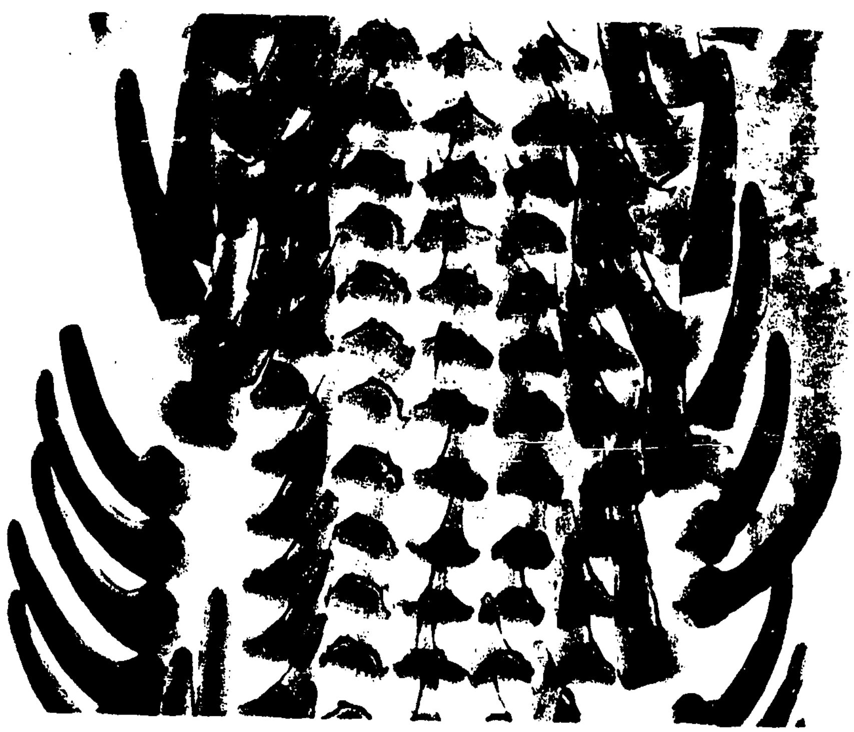


Fig. 2. *Sepia elegans* de Blainville, 1827.

Plate 9

Family Sepiidae

Fig. 1. Single row of radular teeth of *Sepia officinalis* Linné, 1758. (Drawing after Naef, 1923).

Fig. 2. Single row of radular teeth of *Sepia orbigniana* Férussac, 1826. (Drawing after Naef, 1923).

Fig. 3. Single row of radular teeth of *Sepia longipes* Sasaki, 1914 (x80). (Drawing after Sasaki, 1929).

Fig. 4. A portion of the radular ribbon of *Sepia lorigera* Wülker, 1910 (x37). (Drawing after Sasaki, 1929).

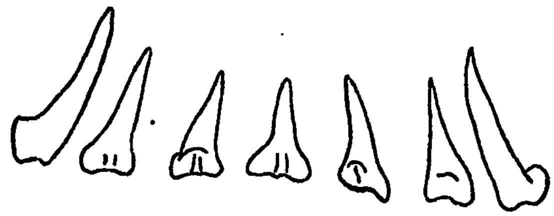


Fig. 1. *Sepia officinalis* Linné, 1758.
(After Naef, 1923)

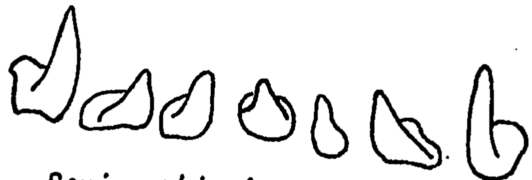


Fig. 2. *Sepia orbigniana* Férussac, 1826.
(After Naef, 1923)

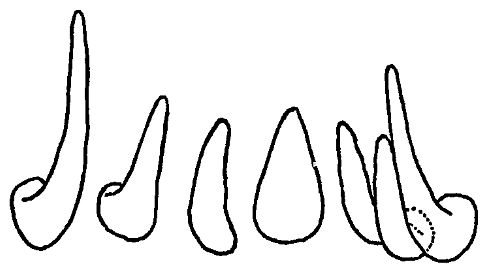


Fig. 3. *Sepia longipes* Sasaki, 1914.
(After Sasaki, 1929)

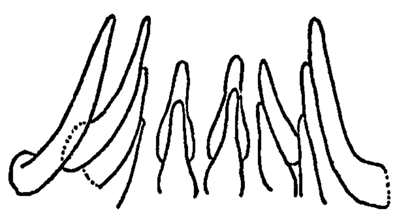


Fig. 4. *Sepia lorigera* Wülker, 1910.
(After Sasaki, 1929)

for study. These were R. *macrosoma* (two specimens), R. *sublevis*, and R. *caroli*, plus a single adult specimen of one heretofore unidentified. Photographs of these are presented in Plate 10, Figures 1 through 4.

Data on these specimens are presented in Table 3, along with data on a larval *Rossia*, the radular ribbon of which is illustrated in Plates 12A and 12B.

Table 3. Mantle length, sex, buccal and radular data for the genus *Rossia* of the Family Sepiolidae.

Species	Mantle Length (mm)	Sex	Buccal Mass Diam. (mm)	Radula Length (mm)	Radula Max. Width (mm)	Radula Min. Width (mm)	Teeth No. of Horiz. Rows	Teeth No. of Longit. Rows
R. *macrosoma*	67	F.	14.5	11.9	2.37	.92	63	7
R. *macrosoma*	41	M.	9.0	8.3	1.80	1.00	74	7
R. *sublevis*	20	M.	6.0	4.5	1.25	.77	51	7
R. *caroli*	35	M.	8.5	7.5	2.10	1.10	56	7
Rossia sp.	35	F.	8.5	6.5	1.50	1.10	54	7
Rossia sp. (Larva)	6	?	2.0	2.0	.93	.18	36	7

By comparing the photograph of R. *macrosoma* with the drawing (Plate 11, Figure 2), it is evident that agreement in many details is lacking. The rachidian tooth in the photograph arises from what may be

Plate 10

Family Sepiolidae

Fig. 1. Photograph of radular teeth of *Rossia macrosoma* d'Orbigny, 1839.

Fig. 2. Photograph of radular teeth of *Rossia caroli* Joubin, 1902.

Fig. 3. Photograph of radular teeth of *Rossia sublevis* Verrill, 1878.

Fig. 4. Photograph of radular teeth of *Rossia* sp.

Fig. 1. *Rossia macrosoma* d'Orbigny, 1839

Fig. 2. *Rossia caroli* Joubin, 1902

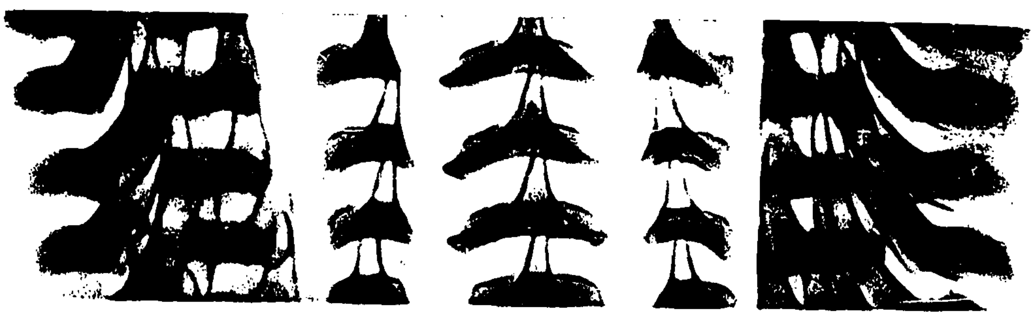


Fig. 3. *Rossia sublevis* Verrill, 1878

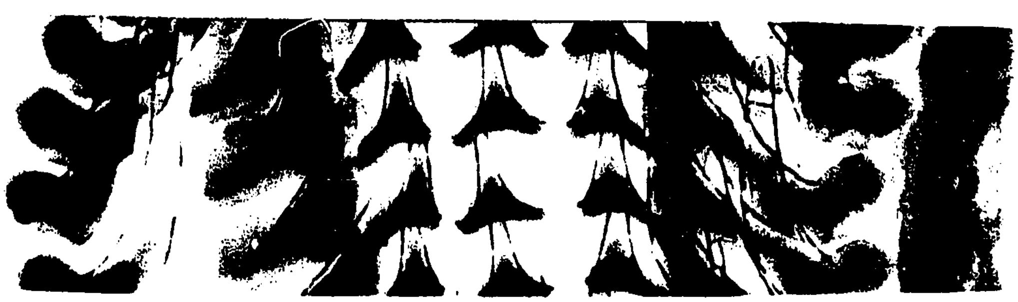


Fig. 4. *Rossia* sp.

termed rounded "shoulders",and a similar condition characterizes the lateral teeth. The cusps of the inner and outer marginal teeth are rounded, not sharply attenuated.

In R. *caroli*, rachidian teeth are tall and arise from a relatively narrow base. The lateral teeth possess cusps which arise from a laterally placed elongated base adjacent to the sharply recurved attenuated cusps of the outer marginals (Plate 10, Figure 2).

Rossia sublevis (Plate 10, Figure 3), differs sharply in the breadth of its rachidian tooth base which is extremely broad. The lateral edges of the rachidian tooth base are pointed in a manner suggesting the formation of a cusp. The bases of the lateral teeth are narrower than those of R. *caroli* or R. *macrosoma*, with no lateral extensions. The cusps of lateral teeth are again equal in size to those of the rachidian teeth. The marginals, although sharply cusped, do not possess the recurvature noted for R. *caroli*.

The radular ribbon of the unidentified species of *Rossia* (Plate 10, Figure 4) is similar in that it has the unicuspid condition of *Rossia* and *Sepia*. It differs from the other species here presented in that the lateral tooth base does not possess the rounded "shoulder" of R. *macrosoma*, the lateral tooth base extension (laterad) of R. *caroli*, nor is it as narrow in base width or breadth as are the tooth bases of the laterals of R. *sublevis*. The angle of the sloping outer edge of the lateral tooth of this radula appears to be intermediate between that of R. *sublevis* and R. *caroli*.

Plate 11

Family Sepiolidae

Fig. 1. Two rows of radular teeth of *Rossia mollicella* Sasaki, 1920. (Original magnification x36). (Drawing after Sasaki, 1929).

Fig. 2. Portion of radular ribbon of *Rossia macrosoma* d'Orbigny, 1839. (Drawing after Naef, 1923)

Fig. 3. Teeth of right half of a single row from the radular ribbon of *Rossia (Austrorossia) antillensis* Voss, 1955. (Drawing after Voss, 1956)

Fig. 4. Portion of radular ribbon of *Rossia (Semirossia) tenera* (Verrill, 1880). (Drawing after Verrill, 1880)

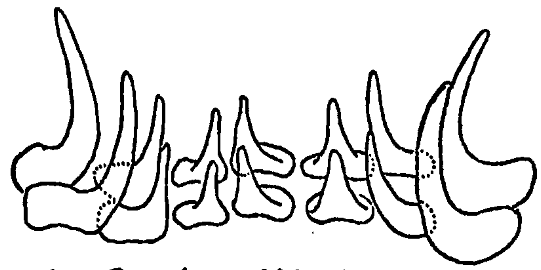


Fig. 1. *Rossia mollicella* Sasaki, 1920.
(After Sasaki, 1929)

Fig. 2. *Rossia macrosoma* d'Orbigny, 1839.
(After Naef, 1923)

Fig. 3. *Rossia (Austrorossia) antillensis*
Voss, 1955. (After Voss, 1956)

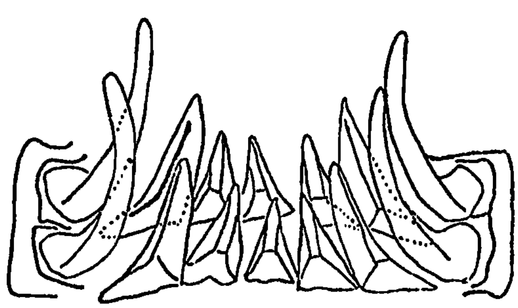


Fig. 4. *Rossia (Semirossia) tenera*
(Verrill, 1880). (After Verrill, 1880)

In addition, R. *macrosoma* was available from the literature (Naef, 1923) (Plate 11, Figure 2), as were R. *mollicella* (after Sasaki, 1929) (Figure 1), R. *antillensis* (after Voss, 1956) (Figure 3) and R. *tenera* (after Verrill, 1880) (Figure 4). A considerable degree of uniformity characterizes these four figures, with the exception of Verrill's (1880) representation of R. *tenera*. Basal plates are developed in the rachidian and other teeth of all four species, with characteristic acute, yet attenuated cusps. It appears that the rachidian is smaller than, or of equal size to, the laterals. In general there appears to be an increase in cusp size of the laterals. The marginal teeth of all four species arise from an elongated base. It must be pointed out that one may wonder at Verrill's (1880) portrayal of the "crystalline" design indicating a leading edge or defined surfaces to all but the marginal teeth.

In Plates 12a and 12b, is represented the radular ribbon of the larval *Rossia*. The entire radular ribbon is shown in 12a and the somewhat damaged condition is due to the extremely small size of the specimen and the radula (Table 3). In Plate 12b can be seen the nascent or growing edge of the radular ribbon (Figure 1). Upon close examination can be seen the faint outlines of developing marginal teeth in the odontogenic tissue. The more developed teeth can be seen to be "unfinished" in developing rows.

Teeth shown in Figure 2 are in a further stage of development, further forward on the radular ribbon. It can be noted that the shape

Plate 12a

Family Sepiolidae

Fig. 1. Photograph of radular ribbon of larval *Rossia* sp. from Chandler Reach region of Bonavista Bay, Newfoundland.

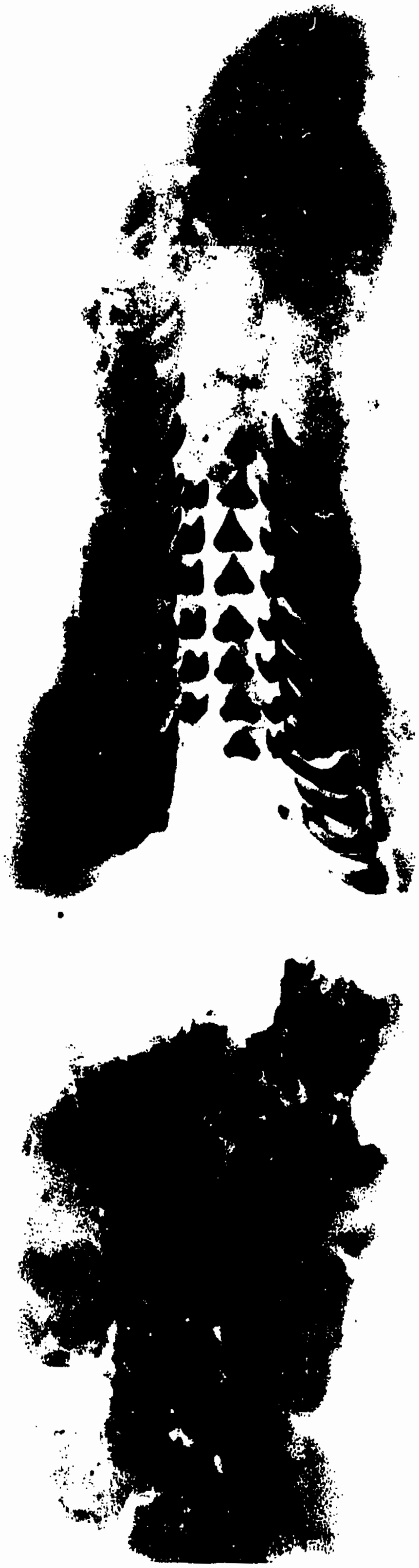


Fig. 1. *Rossia* sp. Complete larval radular ribbon.

Plate 12b

Family Sepiolidae

Fig. 1. Radular ribbon of larval *Rossia* sp. in area of odontogenesis.

Fig. 2. Portion of radular ribbon of larval *Rossia* sp. showing area of greater tooth development.

Fig. 3. Oldest portion of radular ribbon of larval *Rossia* sp.

Fig. 1. Larval *Rossia* sp. (odontogenic area)

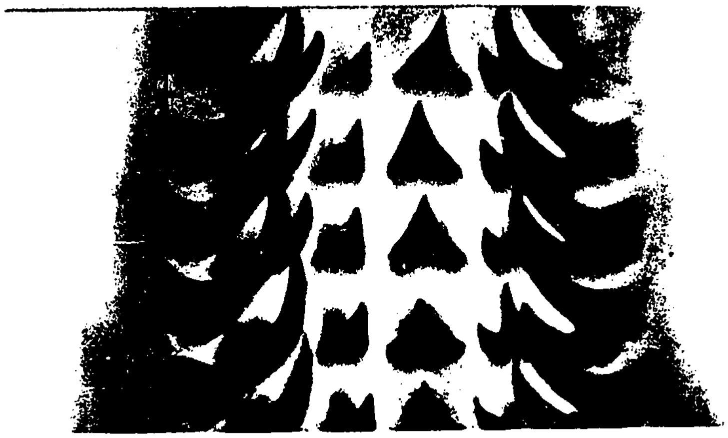


Fig. 2. Larval *Rossia* sp. (tooth development area)

Fig. 3. Larval *Rossia* sp. (oldest radular portion)

of the teeth is more pronounced and the different types of teeth are more easily discernible. Teeth in this area stain to a greater degree than do either those in the newly developing areas or those of the more mature areas. Figure 3 represents the oldest or most forward portion of the radula. Here the teeth do not completely stain. The cusps appear glassy and are translucent. Teeth decrease in size toward the anteriormost tip of the ribbon. Of the species of *Rossia* here figured, this radula most closely resembles that of *Rossia macrosoma*, based on a number of points, most significantly those of the sharply recurved marginal tooth cusps and the rounded "shoulders" of the rachidian tooth bases.

Genus *Sepiola*

Drawings of two species of the Sepiolid genus *Sepiola* were available from the literature, namely, *Sepiola atlantica* (after Adam, 1934) (Plate 13, Figure 1) and *S.* (=*Sepietta*) *oweniana* (after Naef, 1923) (Figure 2). These are similar to one another, and, like the genera *Sepia* and *Rossia*, they demonstrate the unicuspid condition in all teeth, along the elongated bases, particularly in the inner and outer marginals of *S. atlantica* and the inner marginals of *S. oweniana*. Characteristic of this genus is apparently the triangular rachidian tooth.

A single specimen of *S. oweniana* was available and the radular ribbon is illustrated in Plate 14. The data on this specimen are presented in Table 4.

Plate 13

Family Sepiolidae

Fig. 1. Single row of radular teeth of *Sepiola atlantica* d'Orbigny, 1839. (Drawing after Adam, 1934)

Fig. 2. Single row of radular teeth of *Sepiola* (= *Sepietta*) *oweniana* d'Orbigny, 1839. (Drawing after Naef, 1923)

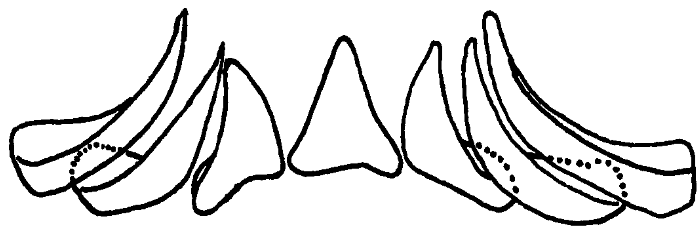


Fig. 1. *Sepiola atlantica* d'Orbigny, 1839. (After Adam, 1934)

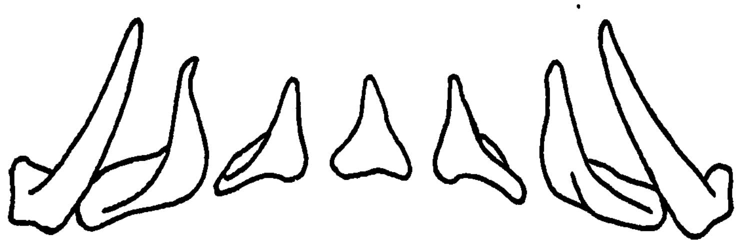


Fig. 2. *Sepiola* (=*Sepietta*) *oweniana* (d'Orbigny, 1839). (After Naef, 1923)

Plate 14

Family Sepiolidae

Fig. 1. Photograph of portion of radular ribbon of *Sepiola* (=*Sepietta*) *oweniana* d'Orbigny, 1839.

Fig. 1. *Sepiola* (=*Sepiette*) *oweniana* d'Orbigny, 1839.

Table 4. Mantle length, sex, buccal and radular data for *Sepiola oweniana* of the Family Sepiolidae.

Species	Mantle Length (mm)	Sex	Buccal Mass Diam. (mm)	Radula Length (mm)	Radula Max. Width (mm)	Radula Min. Width (mm)	Teeth No. of Horiz. Rows	Teeth No. of Longit. Rows
S. oweniana	31	M.	6.5	5.3	1.30	.79	54	7

The photograph of *S. oweniana* (Plate 14) does not agree with Naef's (1923) interpretation of the species. The base of the rachidian is broader, the cusp is more broadly triangular, the marginal teeth are stouter and irregularly broadened more proximally, giving a peculiar scalpel-shape appearance. Both presentations of this species agree basically with respect to laterals, but Naef did not show the sharp medially curved aspect of their cusps characteristic of that presented in Plate 14. They agree with respect to the lateral elongation of the base of the inner marginal teeth, but the cusp of this tooth type is broader and more bluntly rounded at the apex.

Family Loliginidae

Genus *Loligo*

Five specimens of *Loligo pealei* were examined. It is interesting to note that upon examination the slides of the radulae of forms earlier identified as *Lolliguncula brevis*, one of the group did not resemble the others. By re-examining the original specimen, the small differences in sucker dentition, posterior mantle conformation, eye size, and sucker number on the tentacular clubs, it was placed not in the genus *Lolliguncula* but was, in fact, *Loligo pealei*. The specimen in question was approximately the same size as those of the genus *Lolliguncula*, and a cursory examination of a young *Loligo*, and this one was sexually immature, in a catch of *Lolliguncula* would not be sufficient to notice the differences.

A representative illustration of the radular ribbon of *L. pealei* is presented in Plate 15 (Figure 2), along with a drawing of its radular dentition from Williams (1909) (Figure 1). Also represented in Plates 15 and 16 are five additional species of the genus *Loligo*, namely, *L. japonica* (after Sasaki, 1929) (Plate 15, Figure 3), *L. edulis* (after Sasaki, 1929) (Plate 15, Figure 4), *L. forbesi* (after Naef, 1923) (Plate 16, Figure 1), *L. vulgaris* (after Naef, 1923) (Plate 16, Figure 2) and *L. etheridgei* (after Adam, 1954) (Plate 16, Figure 3).

Data on the freshly examined specimens of *Loligo pealei* are presented in Table 5.

Marginal plates are strongly developed in *L. pealei* (Plate 15, Figure 2), as in all other representative members of this genus. Williams (1909) does not figure them so well developed for *L. pealei* (Plate 15, Figure 1).

Table 5. Mantle length, sex, buccal and radular data on the genus *Loligo* of the Family Loliginidae.

Species	Mantle Length (mm)	Sex	Buccal Mass Diam. (mm)	Radula Length (mm)	Radula Max. Width (mm)	Radula Min. Width (mm)	Teeth No. of Horiz. Rows	Teeth No. of Longit. Rows
Loligo pealei								
Specimen #2	233	M.	13	9.0	2.5	1.5	61	7
Specimen #1	213	F.	15	11.3	2.9	1.5	70	7
Specimen #4	193	F.	14	11.0	3.0	1.8	65	7
Specimen #3	192	F.	13	11.0	3.0	1.7	67	7
Specimen #5*	82	F.	8	5.1	1.8	1.1	45	7

*Misidentified *Loligo*, radula damaged at front, or older, end. Formerly *Lolliguncula* #3.

Characteristics of this genus are tricuspid rachidian teeth, bicuspid lateral teeth with elongated tooth bases which extend in a sloping curve toward the base of the rachidian teeth. The bases of the inner marginals are large and broad. The marginal teeth are, in general, appreciably longer than are the other teeth in all six species, but apparently best developed in *L. edulis* (Plate 15, Figure 4). Marginal plates can be described as prominent and well developed.

There is a high degree of similarity among the six species, however Naef's (1923) representation of *Loligo vulgaris* may be questioned as to its accuracy (Plate 16, Figure 2), or is truly exceptional.

Plate 15

Family Loliginidae

Fig. 1. Two rows of radular teeth of *Loligo pealei* (Lesueur, 1821). (Drawing after Williams, 1909)

Fig. 2. Photograph of portion of radular ribbon of *Loligo pealei* (Lesueur, 1821).

Fig. 3. Two rows of radular teeth of *Loligo japonica* (Steenstrup, 1885), the marginal plates not shown on the left side of the ribbon. (Original magnification x40). (Drawing after Sasaki, 1929)

Fig. 4. Two partial rows of radular teeth of *Loligo edulis* Hoyle, 1885. (Original magnification x40). (Drawing after Sasaki, 1929)

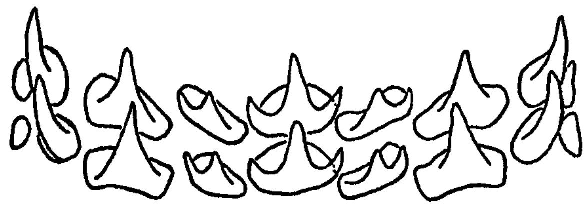


Fig. 1. *Loligo pealei* (Lesueur, 1821).
(After Williams, 1909)

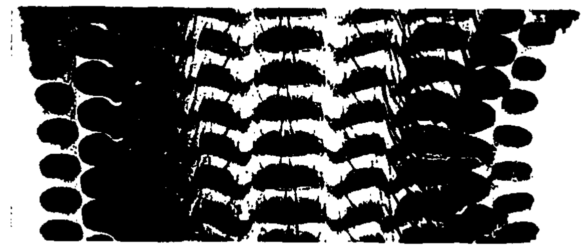


Fig. 2. *Loligo pealei* (Lesueur, 1821).

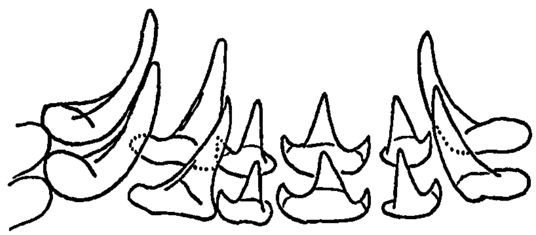


Fig. 3. *Loligo japonica* (Steenstrup, 1885).
(After Sasaki, 1929)

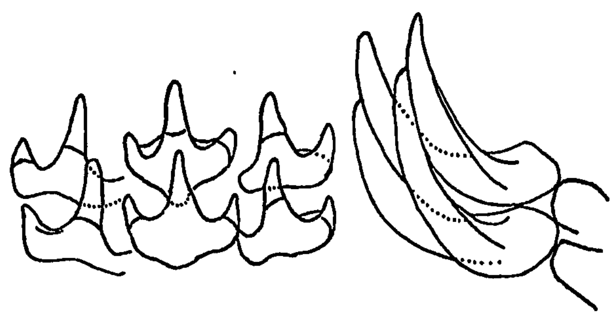


Fig. 4. *Loligo edulis* Hoyle, 1885.
(After Sasaki, 1929)

Plate 16

Family Loliginidae

Fig. 1. Two rows of radular teeth of *Loligo forbesi* Steenstrup, 1856. (Drawing after Naef, 1923)

Fig. 2. Single row of radular teeth of *Loligo vulgaris* Lamarck, 1799. (Drawing after Naef, 1923)

Fig. 3. Single row of radular teeth of *Loligo etheridgei* Berry, 1918. (Original magnification x48). (Drawing after Adam, 1954)

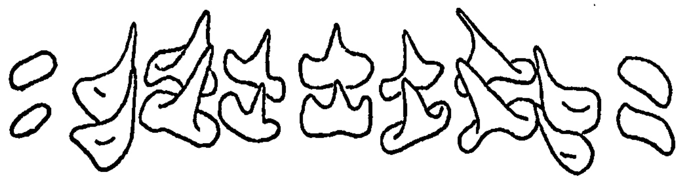


Fig. 1. *Loligo forbesi* Steenstrup, 1856.
(After Naef, 1923)

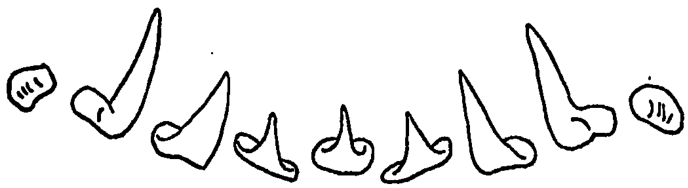


Fig. 2. *Loligo vulgaris* Lamarck, 1799.
(After Naef, 1923)

Fig. 3. *Loligo etheridgei* Berry, 1918.
(After Adam, 1954)

Genus *Doryteuthis*

Three species of *Doryteuthis* were found represented in the literature. These three species, *Doryteuthis singhalensis*, *D. sibogae*, and *D. pickfordae*, are all figured after Adam (1954) and are presented in Plate 17 (Figures 1 through 3) respectively.

Remarkably like *Loligo*, all three species are characterized by tricuspid rachidians, bicuspid laterals with sloping curved bases, and well developed marginal teeth and marginal plates. As observed on a number of occasions in other species, teeth tend to become crowded as the radular ribbon moves forward in the buccal cavity. Resultant displacement and/or overlapping may occur and may explain the V-shaped presentation by Adam (1954) (Plate 17, Figure 3).

Interspecifically, similarities are apparent, yet differences can be easily noted. The rachidian ectocones of *D. singhalensis* and *D. pickfordae* are shorter and less prominent than are those of *D. sibogae*. The same pattern is seen with respect to the ectocones of the lateral teeth. The laterals show differences in the basal length, in that they are shorter in *D. pickfordae*. Lateral teeth are appreciably smaller in both cusp height and basal width than are the rachidian teeth in only *D. pickfordae*. In the other two species the laterals and rachidian teeth are of basically the same cusp height. The marginal teeth are stout and prominent and in *D. singhalensis* appear to be more sharply curved than is the case in either of the other two species represented. The bases from which the inner marginal teeth arise appear to be longer and broader than those of representatives of the genus *Loligo*, with the possible exception of *Loligo etheridgei* (Plate 16, Figure 3).

Plate 17

Family Loliginidae

Fig. 1. Single row of radular teeth of *Doryteuthis singhalensis* (Ortmann, 1891). (Original magnification x80). (Drawing after Adam, 1954)

Fig. 2. Single row of radular teeth of *Doryteuthis sibogae* Adam, 1954. (x80). (Drawing after Adam, 1954)

Fig. 3. Single row of radular teeth of *Doryteuthis pickfordae* Adam, 1954. (Original magnification x150). (Drawing after Adam, 1954)

Fig. 1. *Doryteuthis singhalensis* (Ortmann, 1891). (After Adam, 1954)

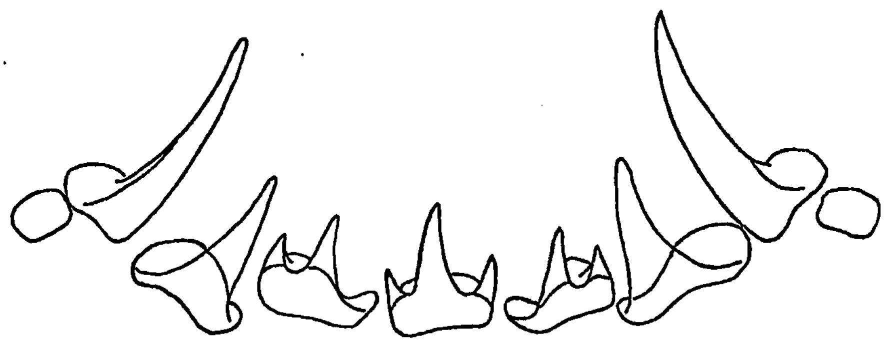


Fig. 2. *Doryteuthis sibogae* Adam, 1954. (After Adam, 1954).

Fig. 3. *Doryteuthis pickfordae* Adam, 1954. (After Adam, 1954)

Genus *Lolliguncula*

Five specimens of *Lolliguncula brevis* were examined (Table 6).

Table 6. Mantle length, sex, buccal and radular data on the genus *Lolliguncula* of the Family Loliginidae.

Species	Mantle Length (mm)	Sex	Buccal Mass Diam. (mm)	Radula Length (mm)	Radula Max. Width (mm)	Radula Min. Width (mm)	Teeth No. of Horiz. Rows	Teeth No. of Longit. Rows
L. brevis								
Specimen #4	78	M.	8	6.1	1.6	0.8	70	7
Specimen #6	65	M.	6.5	5.1	1.7	0.8	65	7
Specimen #7	64	M.	6.5	5.3	1.5	1.1	71	7
Specimen #1	84	F.	8	7.4	2.0	0.5	90	7
Specimen #2	80	F.	8.5	6.5	1.8	0.7	71	7
Specimen #5	77	F.	8	6.3	1.7	0.7	64	7

The radular teeth of *L. brevis* (Plate 18) are characterized by the extreme width of the tricuspid rachidian tooth base so that each sharp lateral cusp or ectocone points laterally and posteriorly. The mesocone arises as a steep, sharp triangle from its base to a height slightly above that of the lateral teeth.

Plate 18

Family Loliginidae

Fig. 1. Photograph of portion of radular ribbon of *Lolliguncula brevis* (de Blainville, 1823)

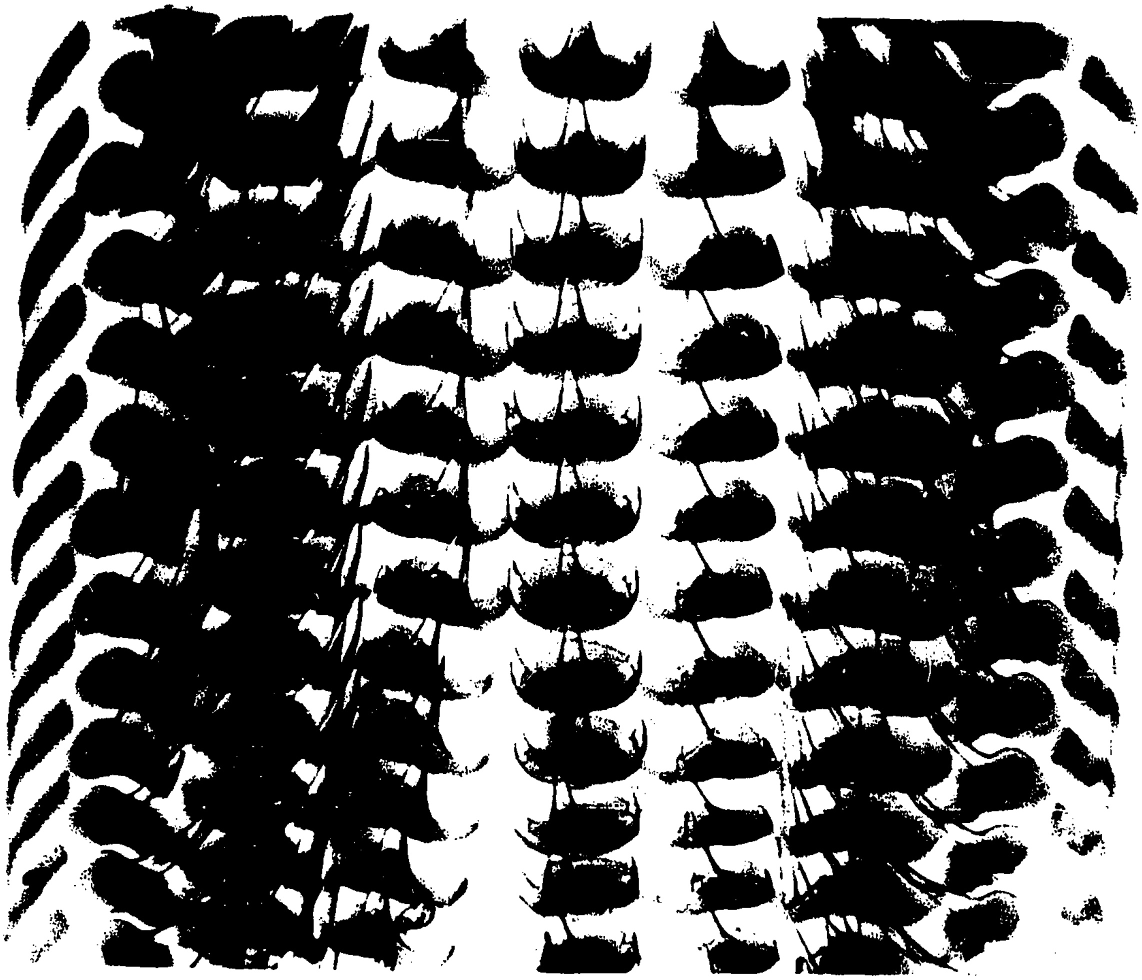


Fig. 1. *Lolliguncula brevis* (de Blainville, 1823)

The bases of the bicuspid lateral teeth are curved and elongated medially to a degree that the distance from the base of the large cusp to the end of the extension is slightly less than the distance from the base of the large cusp to the outer limit of the base. The large cusp of the lateral tooth is directed medially to a slight degree.

The unicuspid inner marginal teeth exhibit a tooth base similar in form to that of the lateral teeth but the medial extension is not as great. The tooth is stout, taller than the laterals and rachidian, and curved medially in direction. The tooth cusp is pointed but not acute, slightly blunt.

The unicuspid marginal teeth are the longest on the radular ribbon. The cusp is roundly acute, the tooth is stout and curves medially and posteriorly from its base.

The marginal plates are well developed, elongated and curved in an anterior direction. The degree of curvature appears to differ to a greater or lesser extent between individuals.

Genus *Sepioteuthis*

In Plate 19, Figure 1, the portion of the radular ribbon of *Sepioteuthis lessoniana* shown exhibits several similarities to that of *Lolliguncula brevis*. The tricuspid rachidian tooth, elongated base of the bicuspid lateral tooth, base extension of the unicuspid inner marginal and medial direction of that cusp, and the slight anterior slant of the marginal plates are strongly reminiscent of *L. brevis*.

Genus *Alloteuthis*

Alloteuthis media, as represented in Plate 19, Figure 2, by a drawing from Naef (1923), presents a homodont condition similar to *Loligo vulgaris*, the *Rossia*'s and *Sepia*'s.

Genus *Uroteuthis*

In Plate 20, Figure 1, is a representation of a single row of radular teeth of *Uroteuthis bartschi* from Adam (1954). Similar to other members of the Family Loliginidae with a heterodont condition of the rachidian and lateral teeth, it does not exhibit the extension of the lateral tooth base. However, the medial direction of the large cusps of the lateral teeth and unicuspid inner marginal teeth is present, as are the well developed marginal plates and stout, curved outer marginal teeth.

Genus *Loliolus*

Loliolus investigatoris (Plate 20, Figure 2) here shows a bicuspid lateral tooth base extension, slightly larger than that of *U. bartschi*. The unicuspid inner marginal teeth are much shorter than the long, sharply curved, acutely pointed, unicuspid outer marginal teeth. The rachidian tooth base appears to be more narrow than *U. bartshi* and other heterodont members of the Loliginidae. Marginal plates are also present.

Plate 19

Family Loliginidae

Fig. 1. Teeth of right half of two rows from the radular ribbon of *Sepioteuthis lessoniana* Férussac, 1826. (Original magnification x20). (Drawing after Sasaki, 1929)

Fig. 2. Portion of radular ribbon of *Alloteuthis media* (Linné, 1758). (Drawing after Naef, 1923)

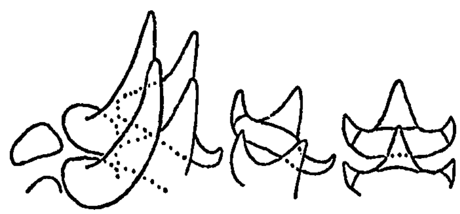


Fig. 1. *Sepioteuthis lessoniana* Férussac, 1826.
(After Sasaki, 1929)

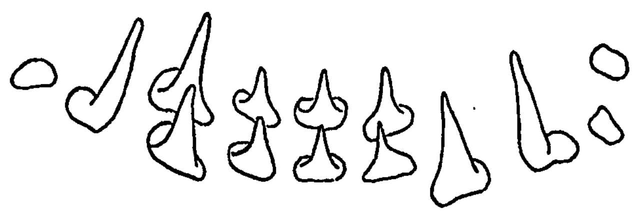


Fig. 2. *Alloteuthis media* (Linné, 1758)
(After Naef, 1923)

Plate 20

Family Loliginidae

Fig. 1. Single row of radular teeth of *Uroteuthis bartschi* Rehder, 1945. (Original magnification x75). (Drawing after Adam, 1954)

Fig. 2. Single row of radular teeth of *Loliolus investigatoris* Goodrich, 1896. (Original magnification x200). (Drawing after Adam, 1954)

Fig. 1. *Uroteuthis bartschi* Rehder, 1945.
(After Adam, 1954)

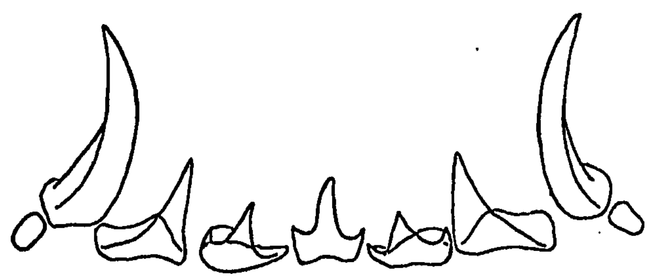


Fig. 2. *Loliolus investigatoris* Goodrich, 1896.
(After Adam, 1954)

Family Enoploteuthidae

Genus *Enoploteuthis*

The genus *Enoploteuthis* is represented in Plate 21 by *E. leptura* (Figure 1) and *E. anapsis* (Figure 2). A single row of teeth from the radular ribbon of *E. leptura* (Figure 1) shows the barely discernible heterodont condition of the rachidian tooth. All the other teeth are slender and very sharply unicuspidate. The inner and taller outer marginal teeth seem to be positioned differently from previously illustrated radular teeth in that the teeth appear to rise sharply and narrowly from a small base and curve medially.

Enoploteuthis anapsis (Figure 2) exhibits a homodont condition in the illustrated single row of radular teeth. However, the tooth cusps are not as acute as in *E. leptura*, the teeth appear to arise from broader bases and are similar in cusp height. Here again, the inner and outer marginal teeth curve medially.

Genus *Abralia*

In Plate 22, the photograph of *A. veranyi* shows the homodont condition of the radular teeth. The tooth cusps are elongate, slender, and sub-acute. The tooth bases are broader and appear to be more square in configuration than the representatives of the genus *Enoploteuthis*. As can be seen in the photograph, the tooth bases are very close together on the radular ribbon and this crowded condition tends to obscure all but general details. It can be seen, however, that the outer marginal teeth are sharply recurved distally.

Plate 21

Family Enoploteuthidae

Fig. 1. Single row of radular teeth of *Enoploteuthis leptura* (Leach, 1817). (Drawing after Roper, 1964).

Fig. 2. Single row of radular teeth of *Enoploteuthis anapsis* Roper, 1964. (Drawing after Roper, 1966).

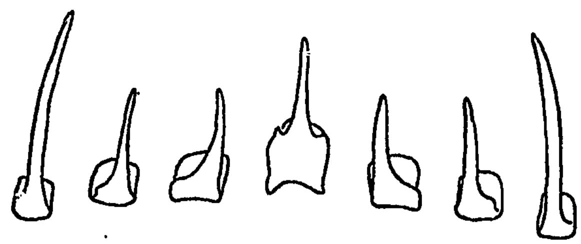


Fig. 1. *Enoploteuthis leptura* (Leach, 1817).
(After Roper, 1964)

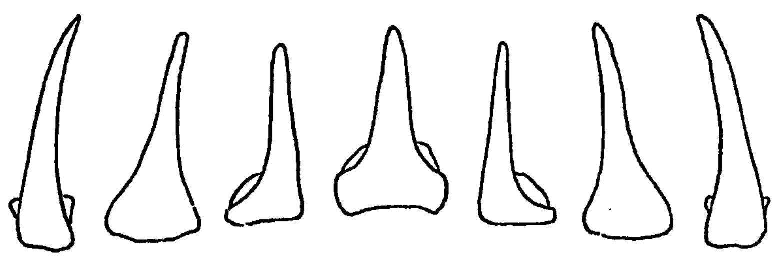


Fig. 2. *Enoploteuthis anapsis* Roper, 1964.
(After Roper, 1966)

Plate 22

Family Enoploteuthidae

Fig. 1. Photograph of portion of radular ribbon of *Abralia veranyi* (Rüppell, 1844).

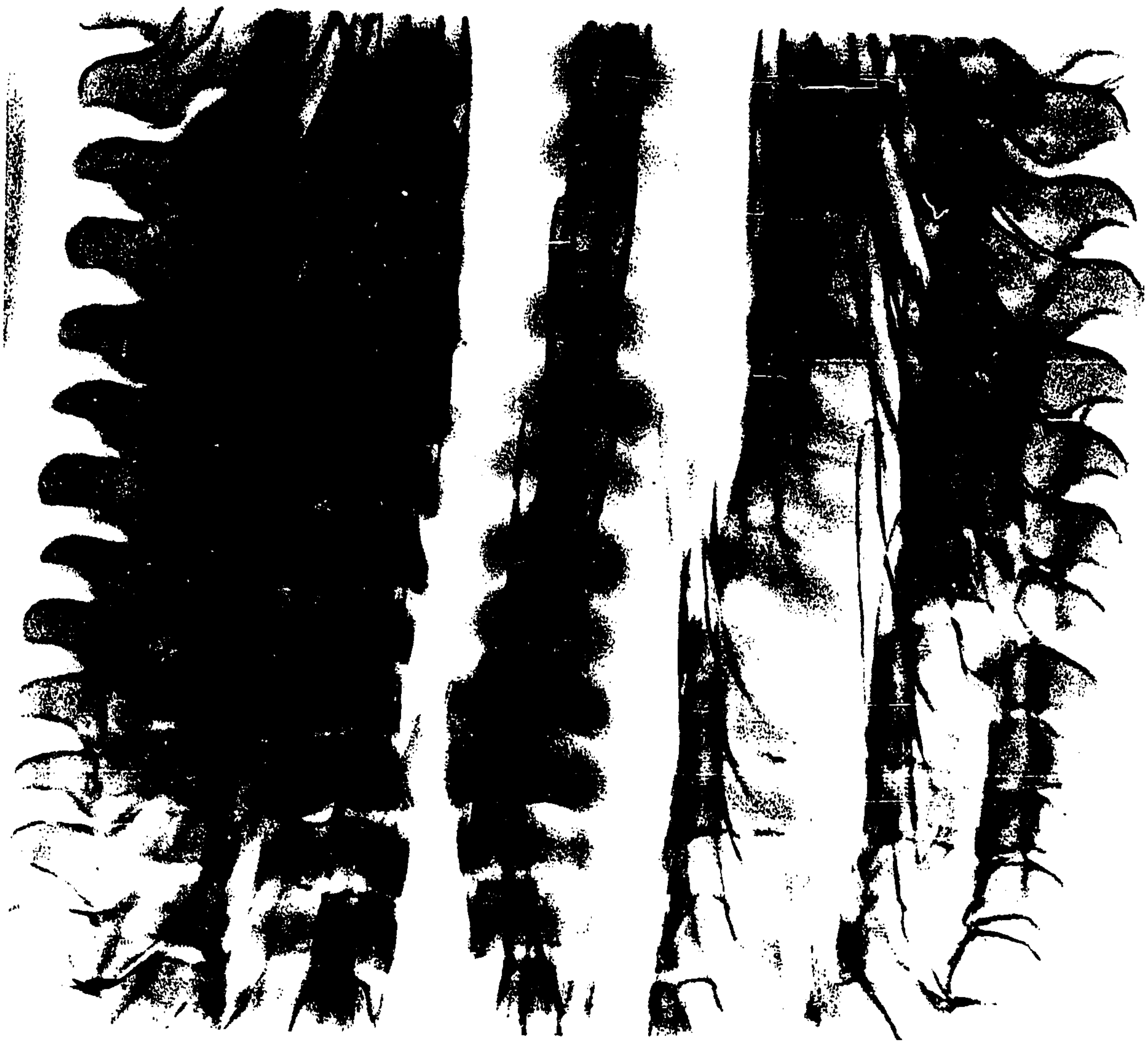


Fig. 1. *Abralia veranyi* (Rüppell, 1844).

Data on the single specimen of *A. veranyi* are presented below in Table 7.

Table 7. Mantle length, sex, buccal and radular data for *Abralia veranyi* of the Family Enoploteuthidae

				Radula			Teeth	
Species	Mantle Length (mm)	Sex	Buccal Mass Diam. (mm)	Length (mm)	Max. Width (mm)	Min. Width (mm)	No. of Horiz. Rows	No. of Longit. Rows
A. veranyi	36	M.	4.5	3.06	.57	.45	86	7

The illustration of a portion of the radular ribbon of *Abralia multihamata* from Sasaki, (1929) also shows a homodont condition (Plate 23, Figure 1). The rachidian tooth of *A. multihamata* has a broadly triangular cusp and a rounded or oval base as do the lateral teeth. None of the teeth show the elongated cusps of *A. veranyi*, *Enoploteuthis lepture*, and *E. anapsis*. The outer marginal teeth of *A. multihamata* are only slightly longer than the other teeth and with the homodont condition these seem to be the only similarities to *A. veranyi*.

Genus *Abraliopsis*

The genus *Abraliopsis* is represented in Figures 2 and 3 of Plate 23. The homodont condition is present as in *Enoploteuthis* and *Abralia*. In *A. gilchristi* the bases of the rachidian and lateral teeth are more square and the elongated outer marginals are somewhat reminiscent

Plate 23

Family Enoploteuthidae

Fig. 1. Two partial rows of teeth from the right half of one radular ribbon of *Abralia multihamata* Sasaki, 1929. (x40). (Drawing after Sasaki, 1929)

Fig. 2. Single row of radular teeth of *Abraliopsis gilchristi* (Robson, 1924). (Drawing after Voss, 1967).

Fig. 3. Two partial rows of teeth from the right half of the radular ribbon of *Abraliopsis hoylei* (Pfeffer, 1884). (x200). (Drawing after Hoyle, 1904)

Fig. 4. Partial rows of teeth from the left side of the radular ribbon of *Pterygioteuthis giardii* Fischer, 1896. (x180). (Drawing after Hoyle, 1904).

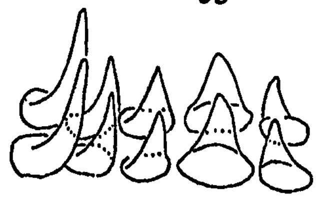


Fig. 1. *Abralia multihamata* Sasaki, 1929.
(After Sasaki, 1929)

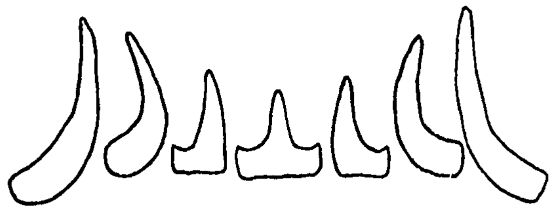


Fig. 2. *Abraliopsis gilchristi* (Robson, 1924).
(After Voss, 1967)

Fig. 3. *Abraliopsis hoylei* (Pfeffer, 1884).
(After Hoyle, 1904)

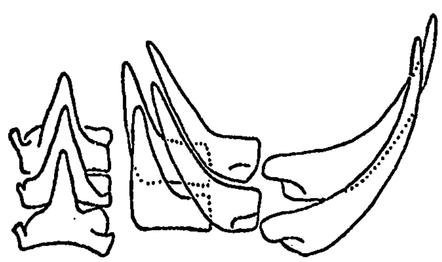


Fig. 4. *Pterygioteuthis giardii* Fischer, 1896.
(After Hoyle, 1904)

of the representatives of the genus *Enoploteuthis* (Plate 21) and *Abralia veranyi* (Plate 22). *Abraliopsis hoylei* as illustrated in the drawing from Hoyle (1904) exhibits the rounded "shoulder" condition of the rachidian tooth and the lateral tooth configuration seen in certain of the *Rossia*'s, so different from *A. gilchristi*. In *A. hoylei* the outer marginals are quite slender and elongated.

Genus *Pterygioteuthis*

Plate 23, Figure 4, represents a portion of the radular ribbon of *P. giardii*, with a somewhat oddly shaped rachidian tooth, not seen heretofore. One side of the rachidian tooth exhibits a small, variably shaped, lateral cusp (ectocone). Lateral extension of the lateral tooth base and saber-like elongation of the outer marginal teeth add to the outstanding differences between these radular teeth and those examined previously.

Family Onychoteuthidae

Genus *Onychoteuthis*

The Family Onychoteuthidae is represented by the genus *Onychoteuthis*, which is here demonstrated by *O. banksi* (Plate 24, Plate 25, Figure 1). Data on the single specimen available are presented in Table 8.

Plate 24 is a photograph which, upon first inspection looks very similar to *R. macrosoma*. A homodont tooth condition, the rounded "shoulders" of both the rachidian and lateral teeth and elongated, acutely cuspid outer marginal teeth enhance this similarity. However, closer examination of the rachidian teeth shows very small lateral cusps (ectocones) on the "shoulders". The lateral teeth show a very slight thickening on the inner or medial shoulder which may suggest a cusp.

Table 8. Mantle length, sex, buccal and radular data for *Onychoteuthis banksi* of the Family Onychoteuthidae.

				Radula			Teeth	
Species	Mantle Length (mm)	Sex	Buccal Mass Diam. (mm)	Length (mm)	Max. Width (mm)	Min. Width (mm)	No. of Horiz. Rows	No. of Longit. Rows
O. banksi	70	M.	5.5	4.5	1.15	.75	45	7

The illustration (Plate 25, Figure 1) does not agree too closely with the photograph. The tooth bases are too broad on the rachidian and lateral teeth and the outer marginal teeth do not show the curvature. I do not know what the dotted lines near the outer marginal tooth bases indicate, as marginal plates are not present in the specimen examined.

Genus *Ancistroteuthis*

The illustration of A. *lichtensteinii* (Plate 25, Figure 2) seems to show radular teeth with a heterodont condition. There would appear to be lateral cusps (ectocones) on the rachidian tooth and small lateral cusps on the lateral teeth. The dotted lines by the outer marginal teeth bases are puzzling. However, the inner and outer marginal teeth are elongated and acutely cuspidate, as with the other represented members of the Family Enoploteuthidae.

Plate 24

Family Onychoteuthidae

Fig. 1. Photograph of portion of radular ribbon of *Onychoteuthis banksii* (Leach, 1817).

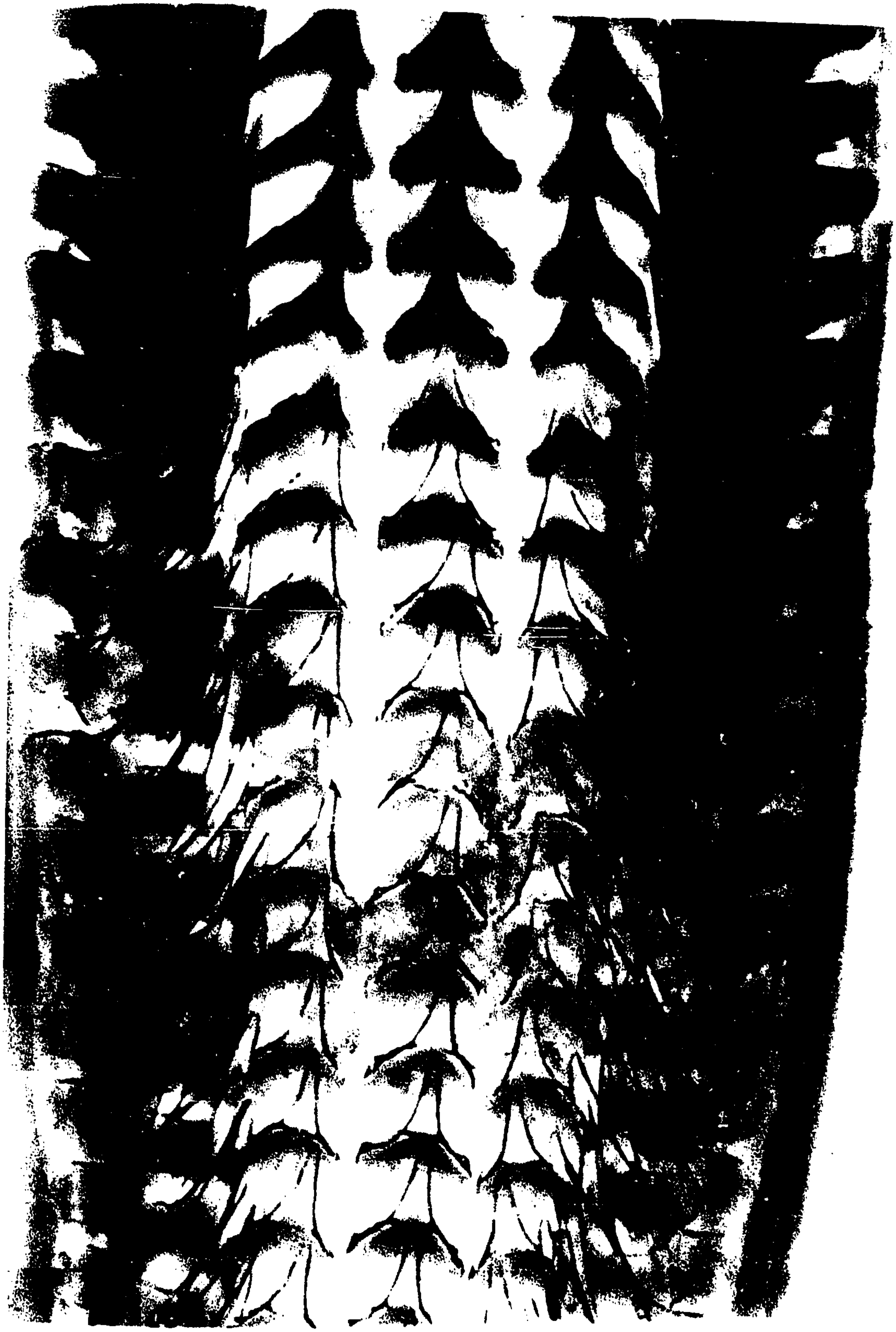


Fig. 1. *Onychoteuthis banksii* (Leach, 1817).

Plate 25

Family Onychoteuthidae

Fig. 1. Portion of radular ribbon of *Onychoteuthis banksii* (Leach, 1817). (Drawing after Naef, 1923)

Fig. 2. Portion of radular ribbon of *Ancistroteuthis lichtensteinii* (d'Orbigny, 1839). (Drawing after Naef, 1923)

Fig. 3. Portion of radular ribbon of *Moroteuthis lönnbergii* Ishikawa & Wakiya, 1914. (Original magnification x40). (Drawing after Sasaki, 1929)

Fig. 4. Partial row of teeth from radular ribbon of *Moroteuthis robusta* (Dall) (Verrill, 1876). (Original magnification x22). (Drawing after Verrill, 1880)

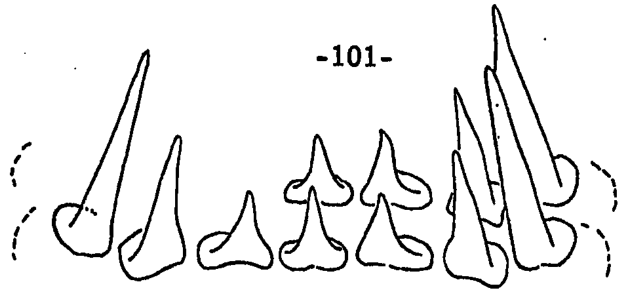


Fig. 1. *Onychoteuthis banksii* (Leach, 1817).
(After Naef, 1923)

Fig. 2. *Ancistroteuthis lichtensteinii* (d'Orbigny, 1839).
(After Naef, 1923)

Fig. 3. *Moroteuthis lonnbergii* Ishikawa & Wakiya, 1914.
(After Sasaki, 1929)

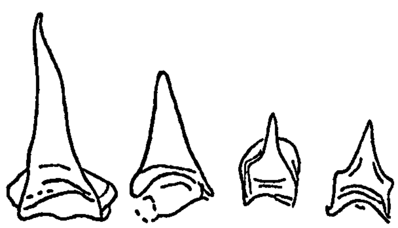


Fig. 4. *Moroteuthis robusta* (Dall) (Verrill, 1876).
(After Verrill, 1880)

Genus *Moroteuthis*

Two species of *Moroteuthis* are represented on Plate 25, Figures 3 and 4. *Moroteuthis lönnbergii* exhibits a heterodont condition as depicted by Sasaki (1929). The lateral teeth display a prominent bicuspid condition and the inner and outer marginal teeth appear to arise from somewhat broad bases. The cusps are shown to be subacute.

Moroteuthis robusta, as depicted by Verrill (1880) shows heterodont radular teeth. However, the lateral cusps (ectocones) of the rachidian tooth are not prominent. The lateral cusp of the lateral tooth appears to be very slight. The inner and outer marginal teeth are shown as broadly triangular in configuration with the outer marginal tooth rather elongate and acutely cuspid.

Family Gonatidae

Genus *Gonatus*

Three members of this genus are illustrated in Plate 26, Figures 1 through 3. The differences between these three representatives are quite striking. *Gonatus fabricii* (Figure 1) is exceptional in that it has only five longitudinal rows of teeth on the radular ribbon. The rachidian tooth is tricuspid, whereas all other teeth are unicuspidate. Rachidian and lateral teeth are of approximately the same height.

The second gonatid *G. magister* (Figure 2), also shows the broad bases of the radular teeth. The rachidian tooth exhibiting a peculiar condition in that it has a single, irregularly-shaped ectocone, similar

Plate 26

Family Gonatidae

Fig. 1. Portion of radular ribbon of *Gonatus fabricii* (Lichtenstein, 1818). (Drawing after Kondakov (1941), as reproduced in Akimushkin, 1963).

Fig. 2. Portion of radular ribbon of *Gonatus magister* Berry, 1913. (Drawing after Kondakov (1941), as reproduced in Akimushkin, 1963).

Fig. 3. Two rows of radular teeth of *Gonatus anonychus* Pearcy & Voss, 1963. (Drawing after Pearcy & Voss, 1963)

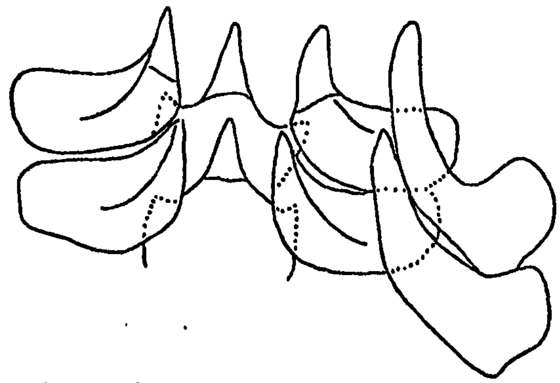


Fig. 1. *Gonatus fabricii* (Lichtenstein, 1818).
((After Kondakov, 1941) from Akimushkin, 1963)

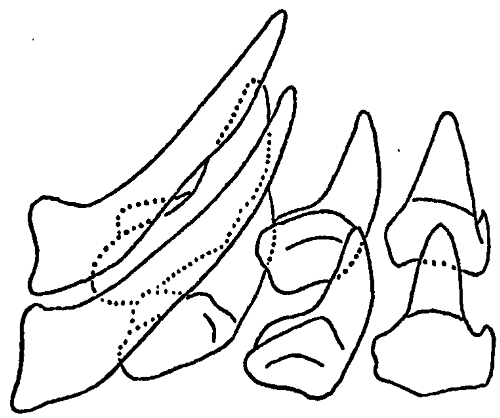


Fig. 2. *Gonatus magister* Berry, 1913.
((After Kondakov, 1941) from Akimushkin, 1963)

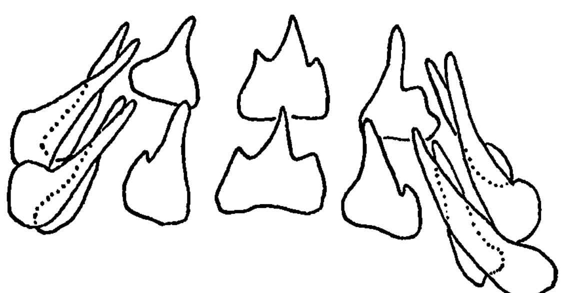


Fig. 3. *Gonatus anonychus* Pearcy & Voss, 1963.
(After Pearcy & Voss, 1963)

to that of *Pterygioteuthis giardii* (Plate 23, Figure 4). Also to be noted is the observation that the outer marginal teeth are stout and roundly unicuspidate.

Gonatus anonychus (Figure 3), the third species of the Family Gonatidae here considered, appears to be heterodont. The bases of the rachidian and lateral teeth are broad. The rachidian mesocone is prominent and acutely cuspid, while ectocones of the rachidian teeth are slight but still apparent. The bicuspid lateral teeth are shown to bear a very rounded prominent inner lateral cusp and a smaller, somewhat variable, outer lateral cusp. The marginal teeth are broad based but more slender and subacute than are those of G. *fabricii* or G. *magister*. They appear to be similar in length to those of G. *magister*.

Family Pholidoteuthidae

Genus *Pholidoteuthis*

The genus *Pholidoteuthis* is represented here by an illustration from Voss (1956) of P. *adami*. The tricuspid condition of the large rachidian tooth and bicuspid condition of the small lateral teeth are apparent. The rachidian mesocone is tall and acute while the ectocones are directed more laterally and are shortened. The lateral teeth are not as broadly based as is the rachidian. The dominant cusp of the lateral teeth is comparatively short, with the lateral surface of the cusp sloping gradually laterad and downward with only a small rise forming the additional cusp. The inner and outer marginal teeth are directed medially and the outer marginal teeth appear to be as tall as the rachidian, (Plate 27, Figure 1).

Plate 27

Family Pholidoteuthidae

Fig. 1. Single row of radular teeth of *Pholidoteuthis adami* Voss, 1956. (Drawing after Voss, 1956)

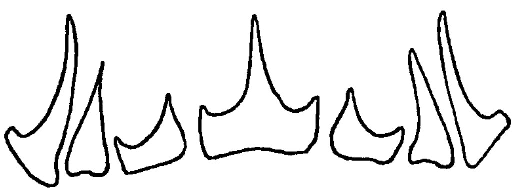


Fig. 1. *Pholidoteuthis adami* Voss, 1956.
(After Voss, 1956)

Family Architeuthidae

Genus *Architeuthis*

Several representatives of this genus are here depicted in Plates 28, 29 and 30. The radular teeth of *A. harveyi*, shown in Plate 28, Figures 1 and 2, from Verrill (1881) display a heterodont condition. The rachidian teeth are tricuspid and possess broad bases. The lateral teeth are bicuspid but the inner marginal tooth of the specimen illustrated in Figure 1 is elongate and bluntly unicuspid, whereas the inner marginal teeth in Figures 2a and 2b are bicuspid and relatively short by comparison. The outer marginal tooth in Figure 1 is broadly triangular in shape, elongate, and the cusp is more blunt than the broadly triangular, and relatively shorter outer marginal teeth in Figures 2a and 2b. In addition the outer marginal teeth in Figures 2a and 2b are acutely unicuspid. The difference in height between the teeth of Figure 1 is quite apparent. In Figures 2a and 2b, the difference in height between the teeth is not as great as that seen in Figure 1, and the cusp heights of the tricuspid rachidian teeth are approximately the same. It should be noted here that the teeth in Figure 2a were from a location more anterior on the radular ribbon than the teeth in Figure 2b, which differ not only in their location but also in that they possess more acute cusps.

In Figure 3 (Plate 28) is presented a portion of a radular ribbon of an unidentified species of the genus *Architeuthis*. It can be readily seen that the heterodont condition is again present. Here, as in Figures 1 and 2, the teeth appear to be similarly broad in their general shape and bluntly cuspidate. The ectocones of the rachidian teeth seen in Figure 3 are shorter than the mesocones and appear to extend laterally and posteriorly. Those in Figures 1 and 2 appear to extend not laterad but only posteriad. The cusps of the bicuspid lateral teeth (Figure 3), particularly those to the left of the rachidian teeth, vary in height and the distance between the cusps is relatively greater than is the situation seen in Figures 1 and 2. However, the lateral teeth in Figure 3 to the right of the rachidian teeth show a greater degree of variation in the lateral inclination of the smaller cusps. Both the inner and outer marginal teeth are broadly triangular in shape and vary in their individual degree of curvature.

In Plate 29, Figures 1 and 2 are illustrations of the heterodont radular teeth of two more unidentified members of the genus *Architeuthis*. Again the heterodont condition is seen in these figures as well as those in Plate 28. The tricuspid rachidian tooth in Figure 1 displays laterally oriented ectocones of approximately equal height, arising from a rather broad base. The cusps of the bicuspid lateral tooth are bluntly rounded, close together and project posteriad from a broad base. The inner and outer marginal teeth exhibit broad bases but it can be seen from Figure 1b that the recurved nature of an inner marginal tooth (=second lateral tooth) and the tooth base are considerably smaller than the configuration exhibited in Figure 1a.

The rachidian teeth of Figure 2a and 2b are similar to those seen in Figure 1. They are tricuspid and broad based. However, in

Figure 2a, the rachidian tooth (from a more posterior location on the radular ribbon) exhibits differences in cusp height in that the ectocones are shorter than the mesocone, while the relative distance between the three cusps appears to be the same as that seen in Figure 2b. The bicuspid lateral tooth in Figure 2a exhibits a more pronounced curvature than that in Figure 2b. Moreover, the lateral tooth illustrated from the more anterior location (Figure 2a) demonstrates a more pronounced curvature in the two cusps than is the condition seen in a corresponding tooth from a more posteriad position (Figure 2b). The inner and outer marginal teeth in Figure 2a exhibit a medially directed curvature in addition to an acute unicuspid condition, while only the inner marginal tooth in Figure 2b is curved similarly.

In Plate 30 (Figures 1 through 3) are presented the radular teeth of three more species of *Architeuthis*, namely, A. *physeteris*, A. *longimanus* and A. *clarkei*. These exhibit similarities and differences when compared with each other and with those on Plates 28 and 29. The rachidian teeth are tricuspid and broad based. In Plate 30, the ectocones of the rachidian teeth are appreciably shorter than the mesocones. The bicuspid lateral teeth in Figure 2 are more blunted than those in Figure 1 and Figure 3a. This is also the situation with regard to the rachidian tooth (Figure 2). The inner and outer marginal teeth exhibit some degree of curvature, medially (Figure 2) or laterally (Figure 1 and Figure 3a and 3b). The inner marginal tooth (=second lateral tooth) is shown in Figure 3b to be sharply recurved, which is not shown in any of the other illustrated architeuthid radular teeth.

Plate 28

Family Architeuthidae

Fig. 1. Partial row of radular teeth of *Architeuthis harveyi* Verrill, 1875. (Drawing after Verrill, 1880).

Fig. 2. a. Isolated teeth from anterior portion of radular ribbon of Logy (Logie) Bay specimen of *Architeuthis harveyi* Verrill, 1875 of 1873. (x18).

b. Isolated teeth from more posterior portion of radular ribbon of Logy (Logie) Bay specimen of *Architeuthis harveyi* Verrill, 1875 of 1873. (x18).

(Both a and b after Verrill, 1881)

Fig. 3. Portion of radular ribbon of Dildo, Trinity Bay, Newfoundland specimen of *Architeuthis* sp. of 1933. (Drawing after Frost, 1934)

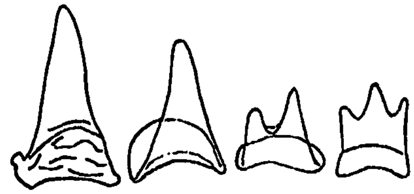


Fig. 1. *Architeuthis harveyi* Verrill, 1875.
(After Verrill, 1880)

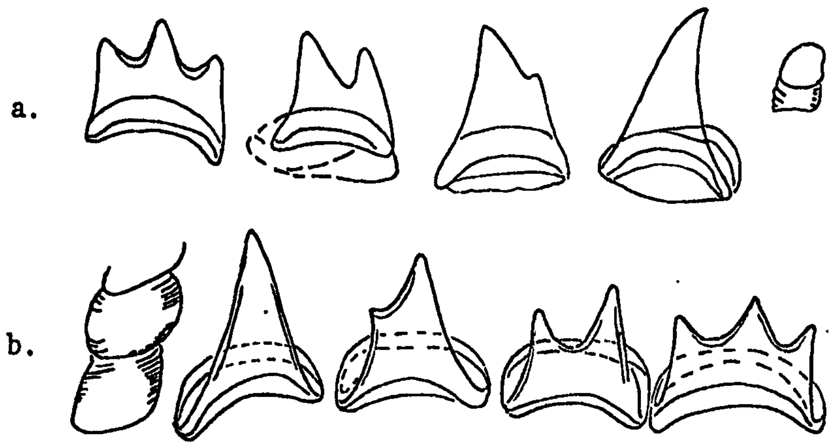


Fig. 2. *Architeuthis harveyi* Verrill, 1875.
(After Verrill, 1881)

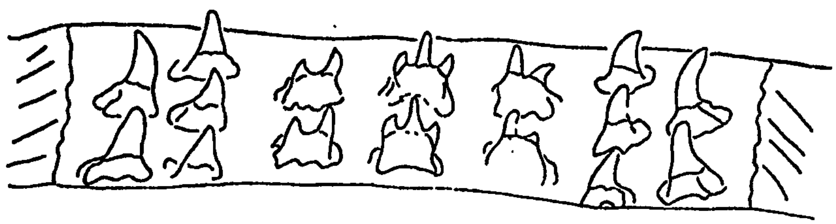


Fig. 3. *Architeuthis* sp. - Dildo, Newfoundland
(After Frost, 1934)

Plate 29

Family Architeuthidae

Fig. 1. a. Radular teeth of Harbour Main, Conception Bay, Newfoundland specimen of 1935 of *Architeuthis* sp.

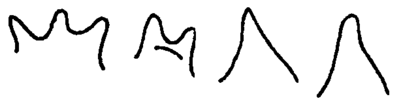
b. Lateral view of second lateral tooth of Harbour Main, Conception Bay, Newfoundland, specimen of 1935 of *Architeuthis* sp.

(Both a and b after Frost, 1935)

Fig. 2. a. Single row of teeth from the posterior portion of the radular ribbon of *Architeuthis* sp. from the Bay of Tateyama, Awa Province, Japan, 1895.

b. Single row of teeth from anterior portion of the radular ribbon near the mouth of *Architeuthis* sp. from the Bay of Tateyama, Awa Province, Japan, 1895.

(Both a and b from Mitsukuri & Ikeda, 1895) a.



b.

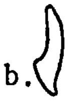


Fig. 1. *Architeuthis* sp. - Harbour Main, Newfoundland. (After Frost, 1935)

a.

b.

Fig. 2. *Architeuthis* sp. (nov.sp.) (After Mitsukuri & Ikeda, 1895)

Plate 30

Family Architeuthidae

Fig. 1. Teeth of left half of a single row from the radular ribbon of *Architeuthis physeteris* Joubin, 1899. (Drawing after Voss, 1956)

Fig. 2. Single row of radular teeth of *Architeuthis longimanus* Kirk, 1888. (Drawing after Kirk, 1888)

Fig. 3. a. Teeth of left half of a single row from the radular ribbon of *Architeuthis clarkei* Robson, 1933.

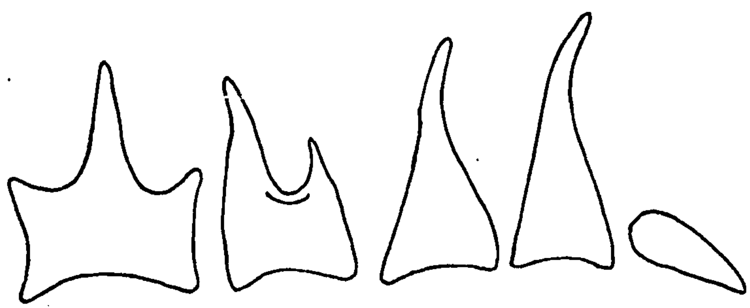
b. Lateral view of second lateral tooth of *Architeuthis clarkei* Robson, 1933.

(Both a and b after Robson, 1933)

Fig. 1. *Architeuthis physeteris* Joubin, 1899. (After Voss, 1956)

Fig. 2. *Architeuthis longimanus* Kirk, 1888. (After Kirk, 1888)

a.



b.

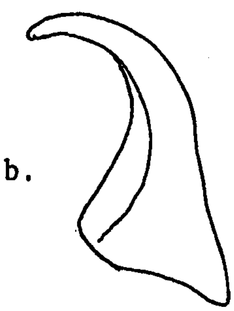


Fig. 3. *Architeuthis clarkei* Robson, 1933. (After Robson, 1933)

Marginal plates are not seen in all the figures presented. Those marginal plates indicated in Plate 28, Figure 2a and 2b differ although they are from the same radular ribbon. The same condition is seen on Plate 29, Figure 2a and 2b.

Also available to this study were five specimens of Architeuthids resulting from the studies of the Family by Dr. F. A. Aldrich. These were identified as *Architeuthis dux* Steenstrup, 1857 (Aldrich, 1968; Aldrich and Aldrich, 1968).

Only two complete radular ribbons were available from these specimens and they are described in Table 9. Measurements of the three incomplete radular ribbons were taken on the portions that were available. Although these specimens were identified as *A. dux*, as noted above, it was found that the radular teeth differed between radular specimens and appeared to be of five different types (Plate 57). The specimens are identified by their place of stranding or landing.

Table 9. Mantle length and radular data for *Architeuthis* sp. from Newfoundland.

Location	Specimen No.	Mantle Length (cm)	Radular Length (mm)	Max. Width (mm)	Min. Width (mm)	No. of Horiz. Rows	No. of Longit. Rows
Lance Cove	1	126.5	59*	11	5.0	94	7
Sweet Bay	2	142.2	56*	11	4.5	96	7
Wild Cove	3	106.7	46	13	4.3	89	7
Chapel Arm	4	126.4	43	15	5.5	83	7
Springdale	5	161.0	34	13	5.3	54	7

*Complete radular ribbons

All five of the Architeuthids have in common seven longitudinal rows of radular teeth, including tricuspid rachidian teeth and bicuspid lateral teeth. However, the specimen from Wild Cove (Plate 57, C) is unique in that it possesses bicuspid inner marginal teeth. Similarly, the specimen from Springdale (Plate 57, E) is characterized by a mediad directed, prominent basal extension on the bases of the inner marginal teeth. This specimen is also unique in that its inner marginal tooth is not inclined toward the midline of the radular ribbon, that is, its cusps are directed to the outer margin or at least are directed posteriorly.

Beyond this, it may be observed that the rachidians differ in certain features in these five specimens. The ectocones of the rachidians are "thorn-like" in two specimens, namely, those from Sweet Bay (Plate 57, D) and Springdale (Plate 57, E). In Plate 57, C, and E, can be seen the rounded cusps of the ectocones of the rachidian teeth of the specimens from Wild Cove and Springdale, respectively. The specimen from Springdale differs in that the bases of the rachidian are short and broad (Plate 57, E), while the specimens from Lance Cove, Chapel Arm and Wild Cove share the characteristic of a broad, but taller base (Plate 57, A, B, C). The ectocones and mesocones of A and B (Lance Cove and Chapel Arm) arise from a portion of the rachidian tooth which is elevated above the upper limit of the base.

The width of the rachidian teeth of the radulae of the five specimens of Architeuthid was measured and the data gained are presented in Table 10. In the presentation of this data, the figures are listed in such a way that the first horizontal row at the front or anteriormost portion of the radular ribbon is designated as Row #1. This was done because the posteriormost portions of the radular ribbons were missing in three of the five specimens. Some teeth, as indicated, were missing. In other instances, some of the rachidian teeth were so poorly oriented that accurate measurements could not be taken and these instances are also noted in the Table.

Table 10. Width (in millimetres) of rachidian teeth of specimens of *Architeuthis* from Newfoundland.

	SPECIMEN				
Anteriormost Row	Lance Cove	Sweet Bay	Wild Cove	Chapel Arm	Springdale
(Row 1)	-*	-**	-*	-**	.660
	-*	-**	.429	-**	.693
	.495	-**	.462	-**	.693
	-*	-**	.462	-**	.759
	.495	-*	.462	-**	-**
	.495	-**	.462	-**	.759
	.495	-**	.462	-**	.759
	.495	-**	.495	-**	.759
	.495	-**	.528	-**	-**
(Row 10)	.495	-**	.528	.462	-**
	.528	-**	.528	.429	-**
	.528	-**	.495	.462	.726**
	.495	-**	.561	.429	.759**
	.594	-**	-*	.396**	.792**
	.594	.495	.561	.396**	.825
	.627	.495	.561	.396**	.825
	.627	.495	.627	.429	.825
	.627	.495	.627	.429	.825
	.627	.495	.627	.429	.891
(Row 20)	.627	.495	.627	.429	.891
	.627	.495	.627	.396**	.891
	.627	.495	.627	.429	.891
	.627	.495	-*	.462	.957
	.627	.495	-*	.462	.957
	.627	.495	-*	.495**	.990
	-*	.495	-*	.495**	.990

Table 10 (continued)

Anteriormost Row	SPECIMEN				
	Lance Cove	Sweet Bay	Wild Cove	Chapel Arm	Springdale
	.627	.528	.660	.495**	.990
	.627	.528	.693	.495**	1.023
	.660	.528	.693	.495**	1.023
(Row 30)	.660	.528	.693	.495**	1.023
	.660	-*	.660	.528	1.023
	.693	.528	.693	.528	1.056
	.693	.528	.693	.528	1.056
	.693	.528	.726	.528	1.089
	.726	.561	.726	.595	1.089
	.726	.561	.726	.627	1.089
	.726	.594	.759	.627	1.089
	.726	.594	.759	.627	1.089
	.726	.627	.792	.627	1.122
(Row 40)	.726	.627	.825	.627	1.122
	.726	.627	.825	.660	1.122
	.759	.627	.825	.660	1.122
	.759	.627	.825	.660	1.155
	.792	.660	.858	.660	1.188
	.792	.660	.858	.660	1.221
	.792	.660	.891	.660	-*
	.792	.660	.891	.660	-*
	.792	.660	.891	.660	-*
	-*	.660	.957	.693	-*
(Row 50)	-*	.693	.957	.693	-*
	.858	.693	.957	.693	-*
	.858	.693	.457	.693	-*
	.858	.693	.957	.726	-*
	.858	.726	.957	.726	-*
	.858	.726	.957	.726	
	.858	.726	.957	.759	
	.891	.726	.990	.759	
	.924	.726	.990	.759	
	.924	.759	.990	.759	
(Row 60)	.924	.759	1.023	.759	
	.924	.759	1.056	.792	
	.924	.759	1.056	.792	
	.957	.759	1.089	.792	
	.957	.759	1.089	.792	
	.990	.759	1.089	.759	
	.990	.759	1.089	.759	
	.990	.759	1.089	.792	
	.990	.759	1.089	.792	
	1.023	.759	1.122	.792	

Table 10 (continued)

Anteriormost Row	SPECIMEN Lance Cove	Sweet Bay	Wild Cove	Chapel Arm	Springdale
(Row 70)	.990	.759	1.122	.759	
	.990	.759	1.122	.759	
	1.056	.759	1.122	-*	
	1.056	.759	1.122	-*	
	1.056	.759	1.122	-*	
	1.056	.759	1.122	-*	
	1.056	.759	1.122	-*	
	1.056	.759	1.155	-*	
	1.056	.759	1.188	-*	
	1.089	.759	1.221	-*	
(Row 80)	1.089	.759	1.221	-*	
	1.089	.759	1.254	-*	
	1.089	.759	1.254	-*	
	1.089	.726	1.254	-*	
	1.023	.660	1.254		
	.957	.660	1.254		
	.957	.726	1.254		
	.957	.660	1.254		
	.825	.561	-*		
	.825	.528	-*		
(Row 90)	.759	.561			
	.759	.363			
	.726	.495			
	.660	.363			
	-**	.363			
		.330			
		.330			

* = Missing or broken

** = Bent or tilted

Family Histioteuthidae

Genus *Histioteuthis*

Two genera from this family are represented in Plates 31, 32 and 33. Both genera display the homodont condition with the single exception of the histioteuthid, *Calliteuthis* (=*Stigmatoteuthis*) sp. (Plate 33, Figure 1). The members of the genus *Histioteuthis* possess marginal plates as indicated in Plate 31, Figures 1 and 2. *Histioteuthis collensii* as figured by Verrill (1880) appears to have a peculiarly shaped marginal plate which looks somewhat like a small, square, unicuspid tooth. The radular teeth of this species are bluntly unicuspidate with the outer marginal tooth recurved laterally. The radular teeth of *H. bonelli* (Plate 31, Figure 2) are more acutely cusped and Naef's (1923) drawing merely suggests the configuration of the marginal plates.

The radular teeth of the illustrated species of the genus *Calliteuthis* are uniformly broad based. The outer marginal teeth are elongate and recurved, and marginal plates are apparently absent. *Calliteuthis elongata* (Plate 32, Figure 2) shows outer marginal teeth recurved to a lesser degree than those of the other species of this genus. With the exception of *C. reversa*, the bases of the lateral and inner marginal teeth exhibit laterally elongated bases reminiscent of some members of the genus *Rossia*. The rachidian teeth show a great deal of variation in shape, ranging from a rounded shoulder in *C. reversa* (Plate 32, Figure 2) to pronounced ectocones seen in Plate 33, Figure 1. The prominent cusps of the rachidian teeth of the various represented calliteuthids are uniformly triangular in shape.

Plate 31

Family Histioteuthidae

Fig. 1. Isolated teeth from right side of radular ribbon of *Histioteuthis collinsii* (Verrill, 1879). (Placed in synonomy with *H. bonelli* (Férussac, 1835), by Clarke, 1966). (Drawing after Verrill, 1880).

Fig. 2. Two rows of radular teeth of *Histioteuthis bonelli* (Férussac, 1835). (Drawing after Naef, 1923).

Fig. 3. Portion of radular ribbon of *Calliteuthis dofleini* (Pfeffer, 1912). (x40). (Drawing after Sasaki, 1929).

Fig. 1. *Histioteuthis collinsii* (Verrill, 1879) (= *H. bonelli* (Férussac, 1835)). (After Verrill, 1880)

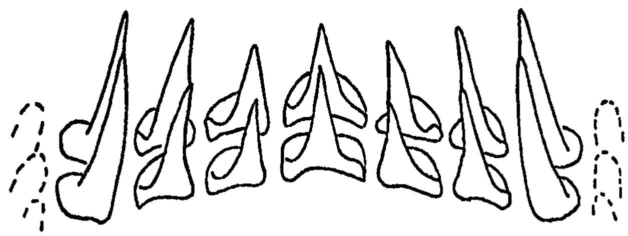


Fig. 2. *Histioteuthis bonelli* (Férussac, 1835). (After Naef, 1923)

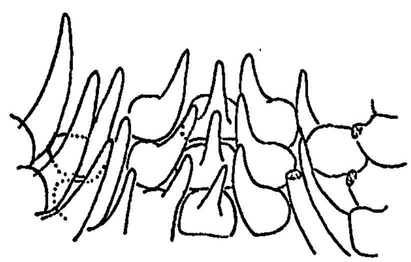


Fig. 3. *Calliteuthis döfleini* (Pfeffer, 1912). (After Sasaki, 1929)

Plate 32

Family Histioteuthidae

Fig. 1. Teeth of right half of a single row from the radular ribbon of *Calliteuthis reversa* Verrill, 1880. (Drawing after Voss & Voss, 1962)

Fig. 2. Teeth of right half of a single row from the radular ribbon of *Calliteuthis elongata* Voss & Voss, 1962. (Drawing after Voss & Voss, 1962)

Fig. 3. Teeth of right half of a single row from the radular ribbon of *Calliteuthis corona* Voss & Voss, 1962. (Drawing after Voss & Voss, 1962)

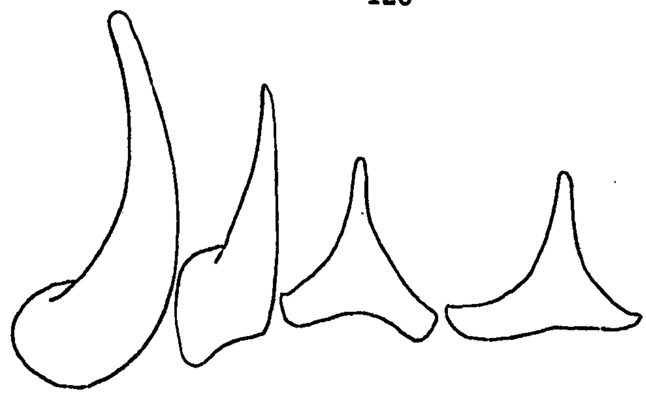


Fig. 1. *Calliteuthis reversa* Verrill, 1880.
(After Voss & Voss, 1962)

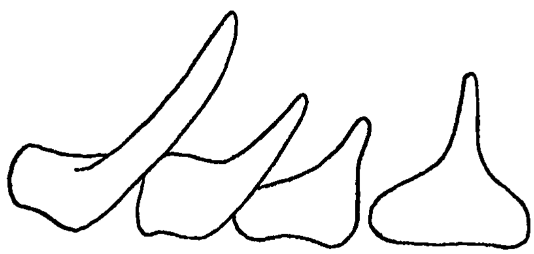


Fig. 2. *Calliteuthis elongata* Voss & Voss, 1962.
(After Voss & Voss, 1962)

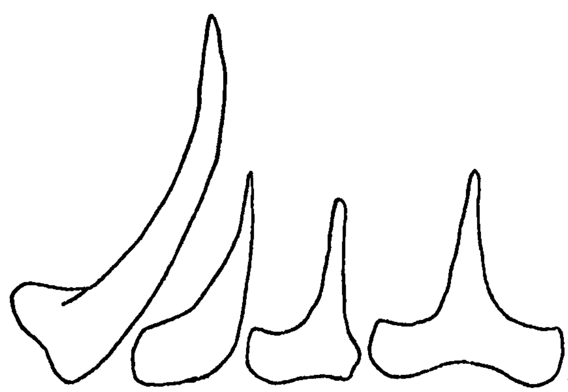


Fig. 3. *Calliteuthis corona* Voss & Voss, 1962.
(After Voss & Voss, 1962)

Plate 33

Family Histioteuthidae

Fig. 1. Single row of radular teeth of *Calliteuthis* (=*Stigmatoteuthis*) sp. (Following Clarke, 1966). (Original magnification x250). (Drawing after Adam, 1954)

Fig. 2. Single row of radular teeth of *Calliteuthis* (=*Meleagroteuthis*) *hoylei* Pfeffer, 1908. (Following Clarke, 1966). (Drawing after Adam, 1954)

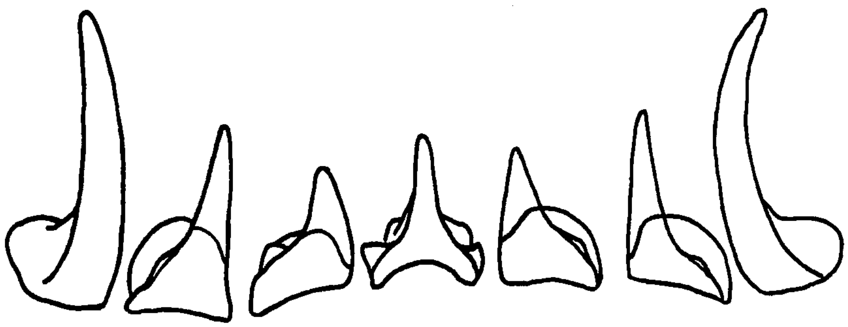


Fig. 1. *Calliteuthis* (=*Stigmatoteuthis*) sp. (After Adam, 1954)

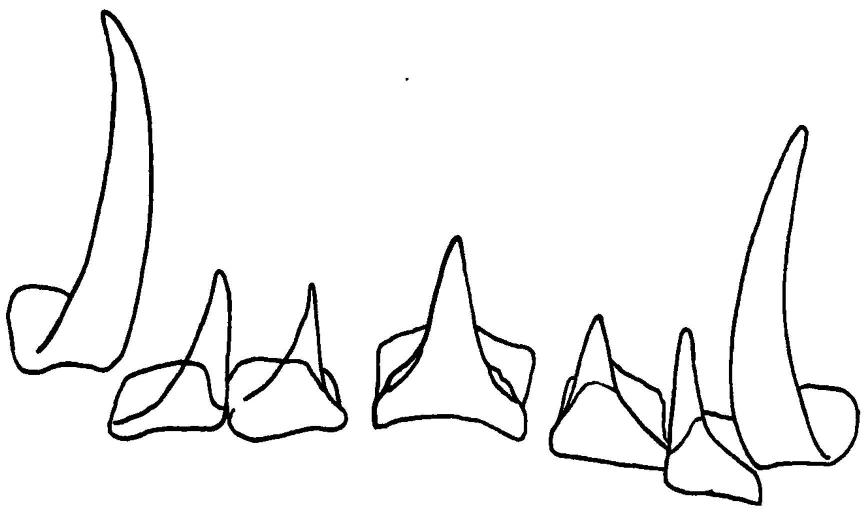


Fig. 2. *Calliteuthis* (=*Meleagroteuthis*) *hoylei* Pfeffer, 1908. (After Adam, 1954)

Family Bathyteuthidae

Genus *Bathyteuthis*

The two members of this genus illustrated here (Plate 34, Figures 1 and 2) exhibit a homodont condition, acute cusps, broad bases, marginal plates and recurved outer marginal teeth.

The radular teeth of *B. bacidifera* (Plate 34, Figure 1) have large, plate-like bases from which the relatively short cusps arise. The rachidian tooth base seen in this illustration is broadly triangular while the lateral and inner marginal teeth show broad lateral extensions of their bases. The lateral and inner marginal teeth curve medially and posteriorly, whereas the height of the lateral teeth appears to approximate that of the rachidian tooth, the inner marginal teeth are taller than these, with the outer marginal teeth elongated and recurved. Marginal plates are shown to be large and well developed.

Bathyteuthis berryi (Plate 34, Figure 2) possesses teeth that are taller and more acutely triangular. The lateral and inner marginal teeth are taller than the rachidian tooth recurved in a lateral direction and show slender lateral extensions of their bases. The outer marginal teeth are more sharply recurved than those in *B. bacidifera*. The marginal plates do not appear to be as large or as well developed as in *B. bacidifera*.

The photograph (Figure 3) shows a portion of the radular ribbon of *Bathyteuthis* sp. While the rachidian tooth strongly resembles that of *B. berryi* (Figure 2) the outer marginal teeth are not as sharply recurved, the marginal plates are larger and better developed, and the

Plate 34

Family Bathyteuthidae

Fig. 1. Single row of radular teeth of *Bathyteuthis bacidifera* Roper, 1968. (Drawing after Roper, 1968).

Fig. 2. Single row of radular teeth of *Bathyteuthis berryi* Roper, 1968. (Drawing after Roper, 1968).

Fig. 3. Photograph of portion of the radular ribbon of *Bathyteuthis* sp.

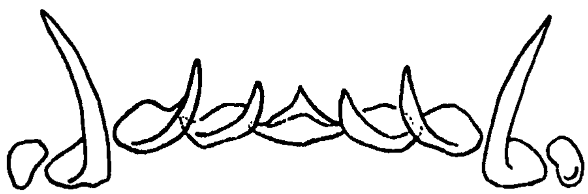


Fig. 1. *Bathyteuthis bacidifera* Roper, 1968.
(After Roper, 1968).

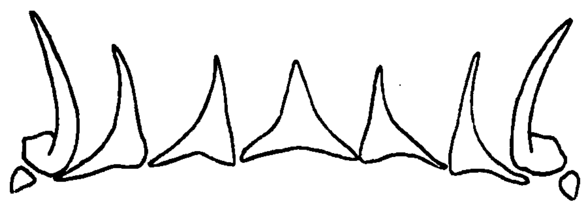


Fig. 2. *Bathyteuthis berryi* Roper, 1968.
(After Roper, 1968).

Fig. 3. *Bathyteuthis* sp.

inner marginal teeth are not as slenderly acute. In all, a total of two specimens of the unidentified *Bathyteuthis* were available. Information on these is presented in Table 11.

Table 11. Mantle length, sex, buccal and radular data for *Bathyteuthis* sp. of the Family Bathyteuthidae.

				Radula			Teeth	
Species	Mantle Length (mm)	Sex	Buccal Mass Diam. (mm)	Length (mm)	Max. Width (mm)	Min. Width (mm)	No. of Horiz. Rows	No. of Longit. Rows
Bathyteuthis sp.	29	F	3.5	3.0	.67	.45	51	7
Bathyteuthis sp.	33	M	3.0	3.2	.55	.42	47	7

Family Batoteuthidae

Genus *Batoteuthis*

The representative of this genus, *Batoteuthis skolops*, (Plate 35, Figure 1), is shown by a portion of a row of radular teeth that are homodont, with large rachidian and outer marginal teeth and comparatively small lateral and inner marginal teeth. The rachidian tooth shows a cusp-like projection on one side of the mesocone. No marginal plates are indicated in the drawing from Young and Roper (1968).

Family Brachioteuthidae

Genus *Brachioteuthis*

In Plate 35, Figure 2, *B. beanii* is represented as having a heterodont condition, broad based teeth and sharply recurved outer

Plate 35

Family Batoteuthidae

Fig. 1. Teeth of left half of a single row from the radular ribbon of *Batoteuthis skolops* Young & Roper, 1968. (Drawing after Young & Roper, 1968)

Family Brachioteuthidae

Fig. 2. Portion of radular ribbon of *Brachioteuthis beanii* Verrill, 1881. (Original magnification x22). (Drawing after Verrill, 1881)

Fig. 1. *Batoteuthis skolops* Young & Roper, 1968.
(After Young & Roper, 1968)

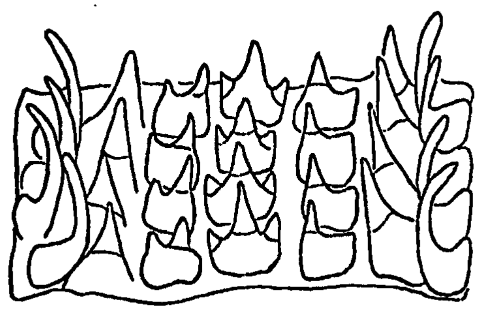


Fig. 2. *Brachioteuthis beanii* Verrill, 1881.
(After Verrill, 1881)

marginal teeth. The bases of the bicuspid lateral and unicuspid inner marginal teeth seem to suggest lateral base extension. The rachidian teeth are tricuspidate with ectocones that are laterally directed and shorter than the mesocone. No marginal plates are present.

Family Ommastrephidae

The family Ommastrephidae is illustrated by representatives of five genera, to be found in Plates 36 through 40 and Plate 41 (Figure2).

Genus *Illex*

The three members of the genus *Illex* are here classified as subspecies of *Illex illecebrosus* (following Aldrich and Lu, 1968b) and are illustrated in Plates 36 and 37, based on earlier sources.

The teeth of this genus are heterodont, broad based, and tall. The rachidian teeth are tricuspid with shorter lateral ectocones. The lateral teeth are bicuspid while the inner and outer marginal teeth are elongate and recurved. Well developed marginal plates are not present in the drawings here reproduced, however, one radular ribbon of *I. illecebrosus coindetii* exhibited well developed marginal plates on both sides of the ribbon for its entire length. This finding was at variance with the other radular ribbons of *I. i. coindetii*. Upon re-examination of the specimens, it was found that one specimen was not a member of the genus *Illex*, but belonged to the genus *Todaropsis*. The similarity between the specimens can be discerned by close examination for the small differences, e.g., tentacle sucker size, etc.

Plate 36

Family Ommastrephidae

Fig. 1. Portion of left side of radular ribbon of *Illex illecebrosus illecebrosus* (Lesueur, 1821). (Drawing after Verrill, 1882)

Fig. 2. Single row of radular teeth of *Illex illecebrosus illecebrosus* (Lesueur, 1821). (Designated as Form C, from Newfoundland, by Zuev, 1966). (Drawing after Zuev, 1966).

Fig. 3. a. Single row of radular teeth of *Illex illecebrosus illecebrosus* as represented by Newfoundland specimens in the collections of Memorial University of Newfoundland.

b. Single row of radular teeth of *Illex illecebrosus illecebrosus* , Form C (Newfoundland), as reproduced from Zuev (1966).

(Both a and b after Aldrich & Lu, 1968b)

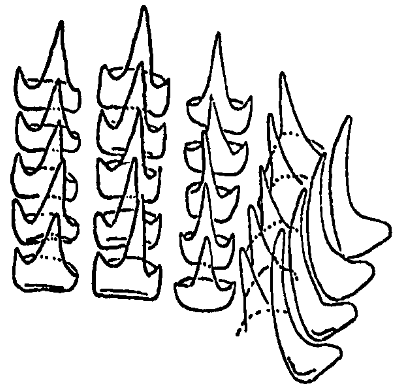


Fig. 1. *Illex illecebrosus illecebrosus* (Lesueur, 1821). (After Verrill, 1882)

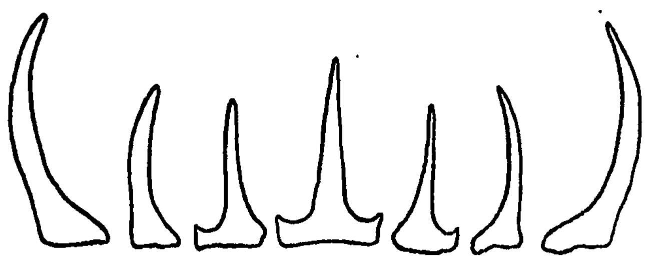


Fig. 2. *Illex illecebrosus illecebrosus* (Lesueur, 1821) (Form C from Newfoundland). (After Zuev, 1966)

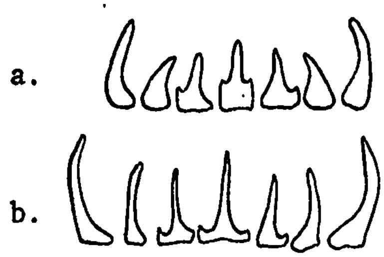


Fig. 3. *Illex illecebrosus illecebrosus* (Lesueur, 1821)

a. As represented in Newfoundland collections at Memorial University.

b. Form C (Newfoundland) - Reproduced from Zuev, 1966.

(After Aldrich & Lu, 1968b)

Plate 37

Family Ommastrephidae

Fig. 1. Two rows of radular teeth of *Illex illecebrosus coindetii* (Verany, 1837). (Drawing after Naef, 1923).

Fig. 2. Photograph of portion of radular ribbon of *Illex illecebrosus illecebrosus* (Lesueur, 1821).

Fig. 3. Photograph of portion of radular ribbon of *Illex illecebrosus coindetii* (Verany, 1837).

Fig. 4. Photograph of portion of radular ribbon of *Illex illecebrosus argentinus* de Castellanos, 1960.

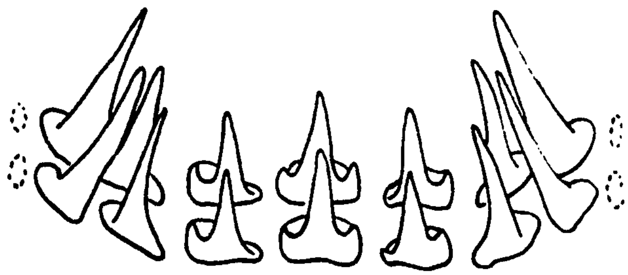


Fig. 1. *Illex illecebrosus coindetii* (Verany, 1837) (After Naef, 1923)

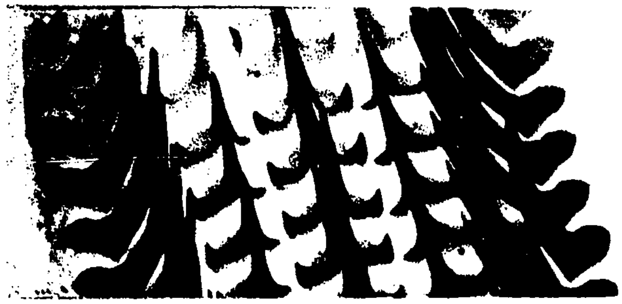


Fig. 2. *Illex illecebrosus illecebrosus* (Lesueur, 1821)

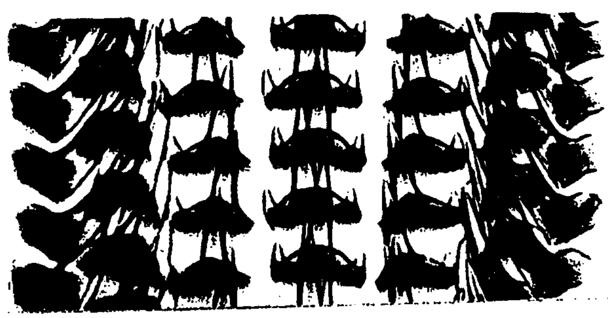


Fig. 3. *Illex illecebrosus coindetii* (Verany, 1837)

Fig. 4. *Illex illecebrosus argentinus* de Castellanos, 1960

Data on the total number of specimens of the genus *Illex* are presented in Table 12 (*Illex illecebrosus illecebrosus*), Table 13 (*I. i. coindetii*) and Table 14 (*I. i. argentinus*).

Table 12. Mantle length, sex, buccal and radular data for *Illex illecebrosus illecebrosus*.

				Radula			Teeth	
Specimen Number	Mantle Length (mm)	Sex	Buccal Mass Diam. (mm)	Length (mm)	Max. Width (mm)	Min. Width (mm)	No. of Horiz. Rows	No. of Longit. Rows
4*	236	F	15.5	10.3	3.1	1.2	52	7
8	231	F	14.5	9.9	3.0	1.4	45	7
3	227	F	14.0	9.1	3.1	1.3	46	7
5	227	F	14.5	9.2	3.1	1.4	47	7
9	214	F	13.0	8.6	3.0	1.0	49	7
1	211	F	11.5	9.0	3.0	1.2	46	7
10	210	F	12.5	9.4	2.8	1.2	44	7
2	207	F	11.5	8.8	2.8	1.2	45	7
6	203	F	13.0	8.5	3.0	1.3	43	7
7	192	F	10.5	8.2	2.8	1.0	44	7
14	230	M	14.5	10.2	2.8	1.2	48	7
12	220	M	11.5	8.7	2.9	1.3	43	7
13	218	M	12.5	9.3	2.9	1.5	46	7
18	218	M	14.5	9.8	3.0	1.5	44	7
16	213	M	13.5	8.8	3.0	1.4	44	7
19	207	M	13.0	9.0	3.0	1.5	46	7
15	199	M	12.5	8.3	2.5	1.4	43	7
11	198	M	11.0	8.3	2.6	1.3	45	7
20	198	M	11.5	8.5	2.8	1.2	45	7
17	161	M	9.5	6.5	2.5	1.0	41	7

*Arranged in order of decreasing mantle length and grouped according to sex.

Table 13. Mantle length, sex, buccal and radular data for *Illex illecebrosus coindetii*.

Specimen Number	Mantle Length (mm)	Sex	Buccal Mass Diam. (mm)	Radula Length (mm)	Radula Max. Width (mm)	Radula Min. Width (mm)	Teeth No. of Horiz. Rows	Teeth No. of Longit. Rows
21*	160	F	12.0	9.0	2.5	1.5	47	7
6	123	F	12.0	7.5	2.3	1.1	50	7
8	103	F	9.0	6.3	2.0	1.0	45	7
20	90	F	8.0	5.8	1.6	1.1	47	7
7	89	F	8.5	6.0	2.0	0.9	45	7
9	88	F	8.5	5.3	1.9	0.9	46	7
10	82	F	8.0	5.3	1.9	0.9	45	7
1	160	M	16.5	12.9	2.5	2.0	58	7
2	154	M	14.5	12.8	2.5	1.8	65	7
22	153	M	15.5	11.0	2.3	2.0	62	7
3	144	M	16.5	12.5	2.3	1.5	76	7
4	135	M	15.0	10.0	2.1	1.5	59	7
12	116	M	11.5	8.3	2.3	1.1	50	7
11	115	M	12.0	8.2	2.3	1.0	47	7
19	111	M	13.0	9.0	1.8	1.3	59	7
14	103	M	11.0	7.1	2.0	1.0	46	7
13	102	M	11.5	7.0	2.3	1.0	47	7
15	91	M	9.0	6.5	2.0	0.7	46	7
16	87	M	7.5	5.9	2.0	0.9	45	7
18	78	M	6.0	4.3	1.3	0.5	41	7
17	75	M	8.0	4.8	1.5	0.6	42	7

*Arranged in order of decreasing mantle length and grouped according to sex.

Table 14. Mantle length, sex, buccal and radular data for *Illex illecebrosus argentinus*.

Specimen Number	Mantle Length (mm)	Sex	Buccal Mass Diam. (mm)	Radula Length (mm)	Radula Max. Width (mm)	Radula Min. Width (mm)	Teeth No. of Horiz. Rows	Teeth No. of Longit. Rows
3*	197	F	15.0	9.9	2.6	1.8	48	7
2	175	F	13.5	9.0	2.6	1.6	43	7
1	163	M	14.0	9.8	2.5	1.8	49	7

*Arranged in order of decreasing mantle length and grouped according to sex.

The data on the width of radular rachidian teeth of the three individuals representing the three subspecies are presented in the following table (Table 15).

Table 15. Comparison of rachidian tooth measurements (width) of intact complete radulae of three subspecies of *Illex illecebrosus*.

Illex i. illecebrosus (#17)		*I. i. coindetii* (#1)		*I. i. argentinus* (#1)	
ML = 161 mm RL = 6.5 mm Sex: Male Rachidian tooth width		ML = 160 mm RL = 12.9 mm Sex: Male Rachidian tooth width		ML = 163 mm RL = 9.8 mm Sex: Male Rachidian tooth width	
Row No.	Width (mm)	Row No.	Width (mm)	Row No.	Width (mm)
1	.292 .279 .285	1	.279 .255 .255	1	.279 .279 .307

Table 15 (continued)

Illex i. illecebrosus (#17)		*I. i. coindetii* (#1)		*I. i. argentinus* (#1)	
Row No.	Width (mm)	Row No.	Width (mm)	Row No.	Width (mm)
	.315		.255		.315
	.315		.255		.337
	.315		.300		.337
	.315		.315		.345
	.322		.322		.358
	.315		.337		.360
10	.315	10	.345	10	.360
	.315		.345		.360
	.307		.345		.367
	.300		.345		.367
	.285		.345		.372
	.279		.345		.360
	.279		.345		.360
	.262*		.345		.360
	.255		.345		.367
	.279		.345		.372
20	.268	20	.345	20	.375
	.255		.300*		.367
	.255		.300*		.367
	.247		.285*		.367
	.240		.315*		.360
	.240		.345		.360
	.240		.345		.360
	.240		.360		.357
	.225		.360		.360
	.225		.375		.345
30	.210	30	.360	30	.345
	.210		.360		.345
	.202		.360		.345
	.195		.360		.334
	.195		.360		.330
	.187		.360		.330
	.180		.352		.322
	.172		.352		.322
	.165		.352		.322
	.165		.345		.315
	.165	40	.345	40	.315
41	.150		.345		.312
			.337		.300
			.330		.300
			.330		.292

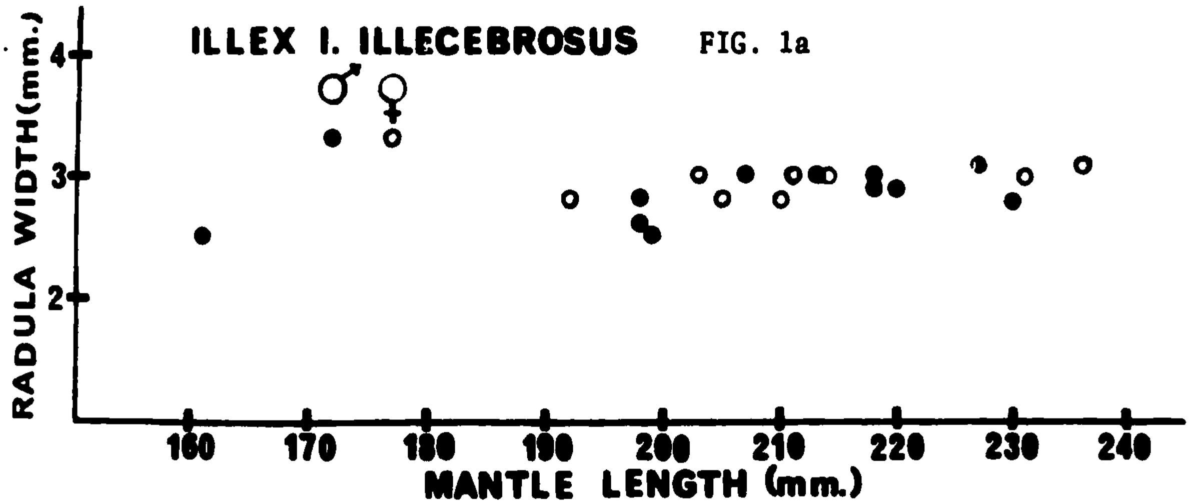
Table 15 (continued)

Illex i. illecebrosus (#17)		*I. i. coindetii* (#1)		*I. i. argentinus* (#1)	
Row No.	Width (mm)	Row No.	Width (mm)	Row No.	Width (mm)
			.330		.285
			.330		.285
			.330		.285
			.315		.255*
			.315	49	.255*
		50	.315		
			.315		
			.315		
			.315		
			.300		
			.307		
			.300		
			.300		
		58	.285		
RL:ML = 1:2.47		RL:ML = 1:1.24		RL:ML = 1:1.66	

ML = Mantle Length
RL = Radular Length

*Tilted

The data on radular length and width are plotted against mantle length of *Illex i. illecebrosus* in Figures 1a and 1b. In Figures 2a and 2b are plotted the observed values for the same variables for *I. i. coindetii*. The radular length and radular width are expressed as percentages of the mantle length in Figures 3a and 3b for *I. i. illecebrosus* and in Figures 4a and 4b for *I. i. coindetii*. The computed radular length:radular width indices (RL/RW) for *I. i. illecebrosus* are presented in Figure 3c and for *I. i. coindetii* in Figure 4c.



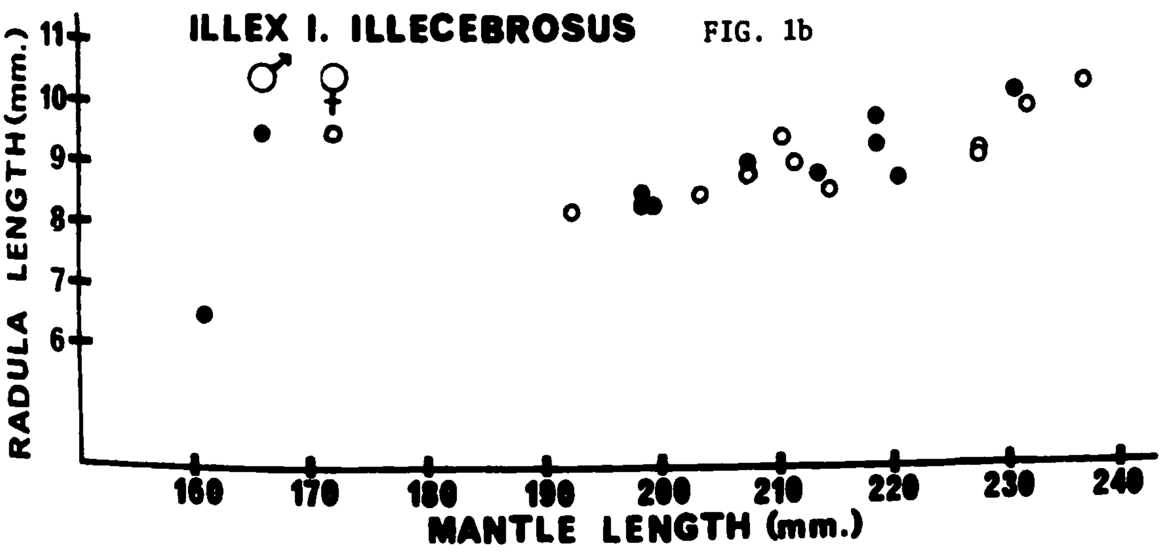
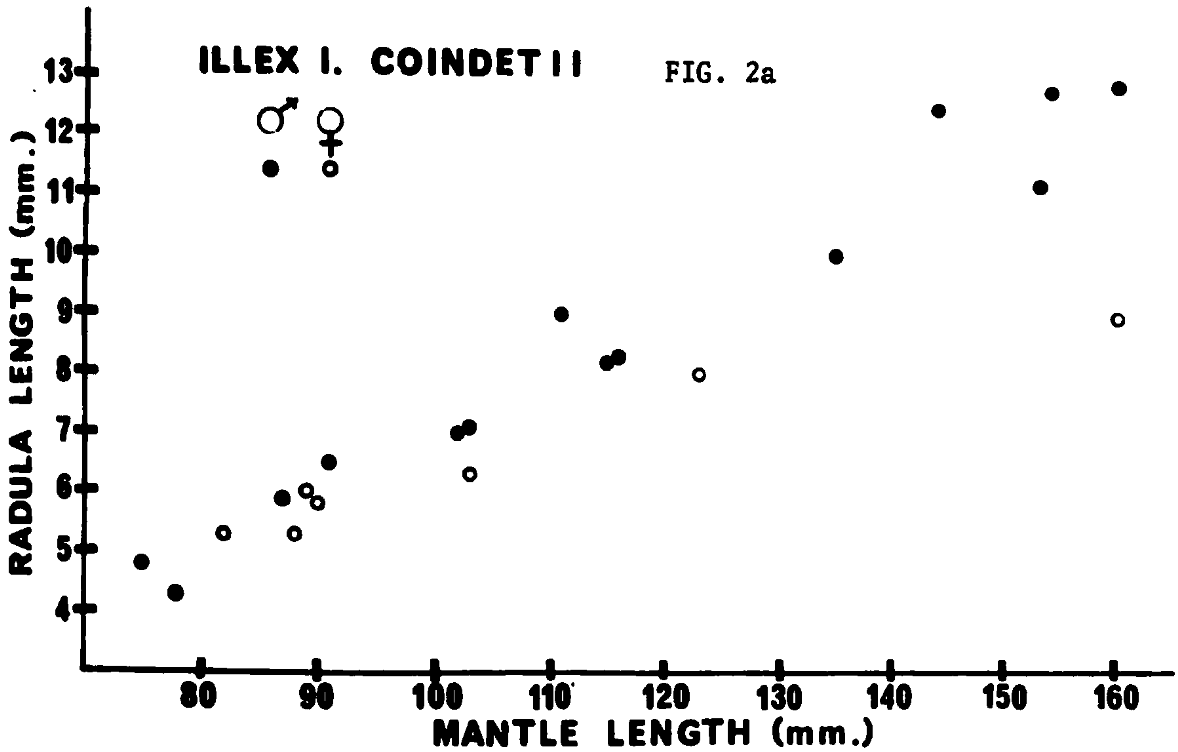


Fig. 1a Relationship between mantle length and radular width of *Illex illecebrosus illecebrosus*.

Fig. 1b Relationship between mantle length and radular length of *Illex illecebrosus illecebrosus*.



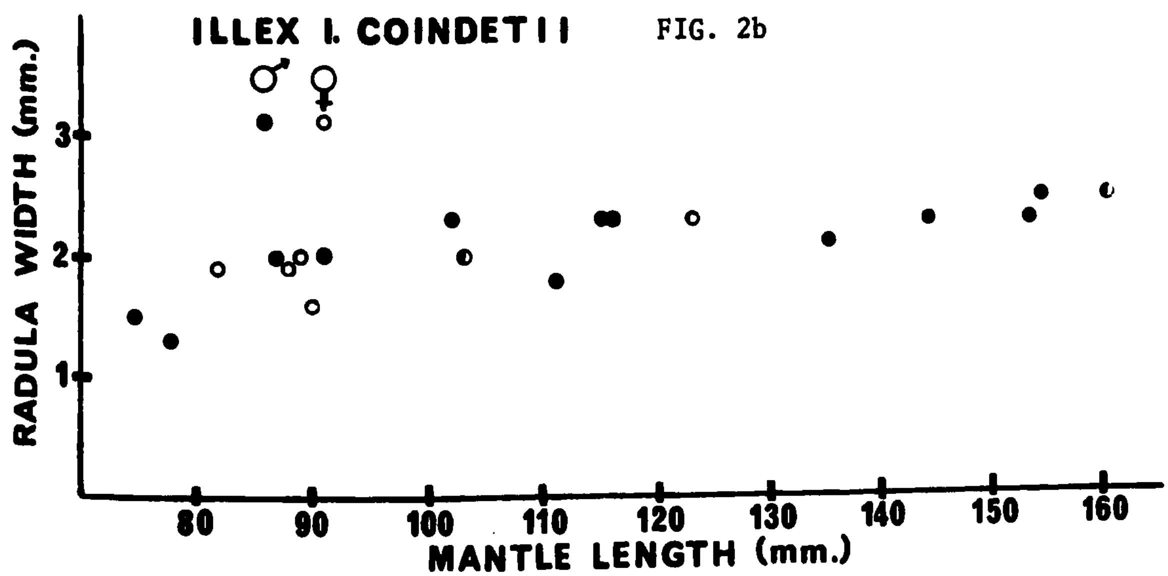


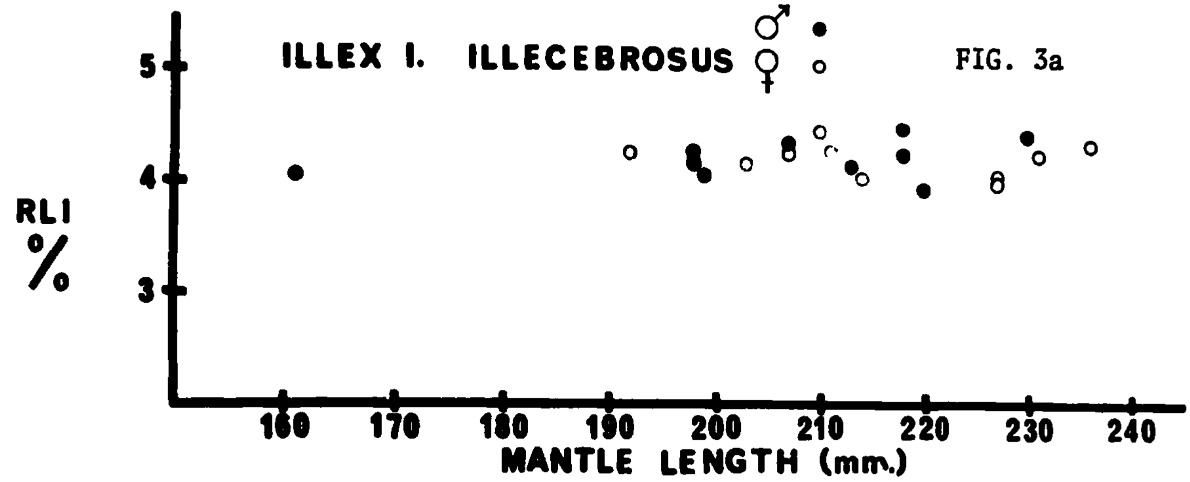
Fig. 2a. Relationship between mantle length and radular length of *Illex illecebrosus coindetii*.

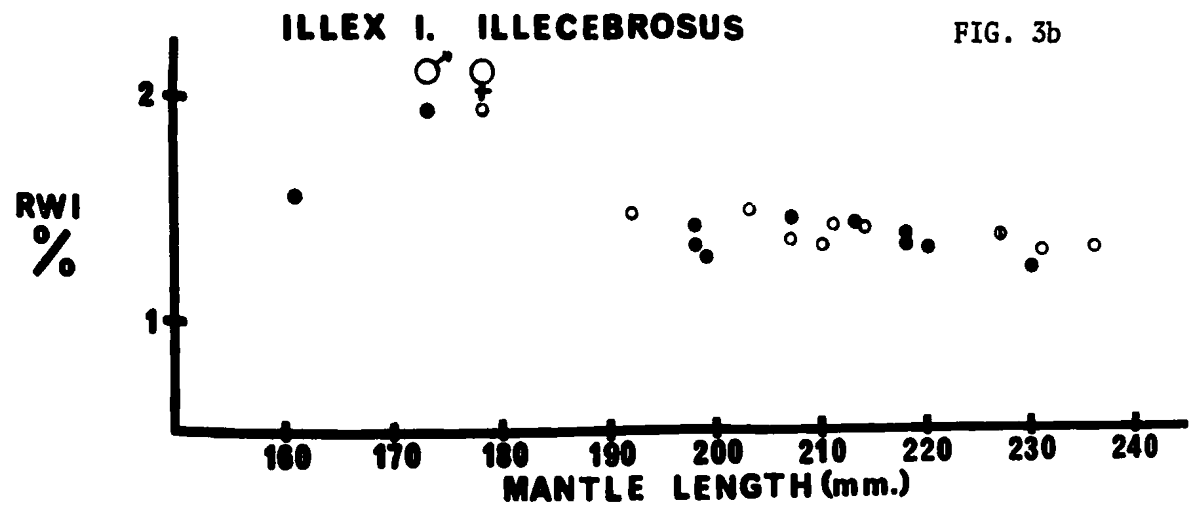
Fig. 2b. Relationship between mantle length and radular width of *Illex illecebrosus coindetii*.

Fig. 3a. Relationship between mantle length and radular length index in *Illex illecebrosus illecebrosus*.

Fig. 3b. Relationship between mantle length and radular width index in *Illex illecebrosus illecebrosus*.

Fig. 3c. Relationship between mantle length and radular length-radular width ratio in *Illex illecebrosus illecebrosus*.


ILLEX I. ILLECEBROSUS
♂ ●
♀ ○
FIG. 3a
RLI %
5
4
3
160
170
180
190
200
210
220
230
240
MANTLE LENGTH (mm.)


ILLEX I. ILLECEBROSUS
FIG. 3b
♂ ♀
RWI %
2
1
160
170
180
190
200
210
220
230
240
MANTLE LENGTH (mm.)

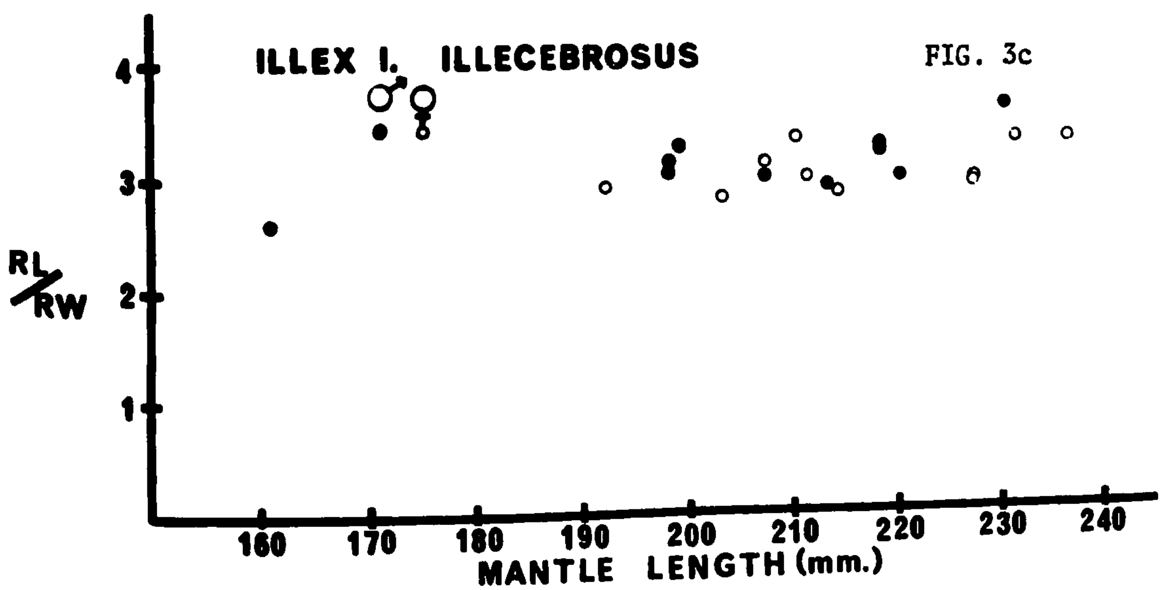

ILLEX I. ILLECEBROSUS
FIG. 3c
♂ ♀
RL/RW
4
3
2
1
160
170
180
190
200
210
220
230
240
MANTLE LENGTH (mm.)

Fig. 4a. Relationship between mantle length and radular length index in *Illex illecebrosus coindetii.*

Fig. 4b. Relationship between mantle length and radular width index in *Illex illecebrosus coindetii.*

Fig. 4c. Relationship between mantle length and radular length-radular width ratio in *Illex illecebrosus coindetii.*

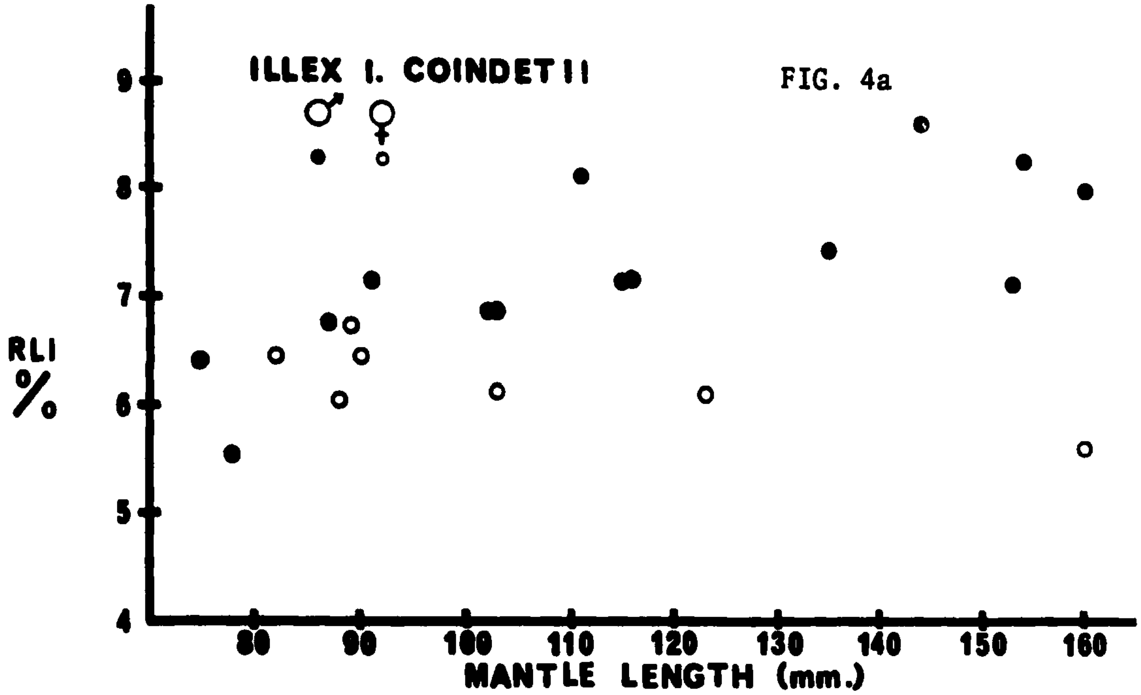


FIG. 4a

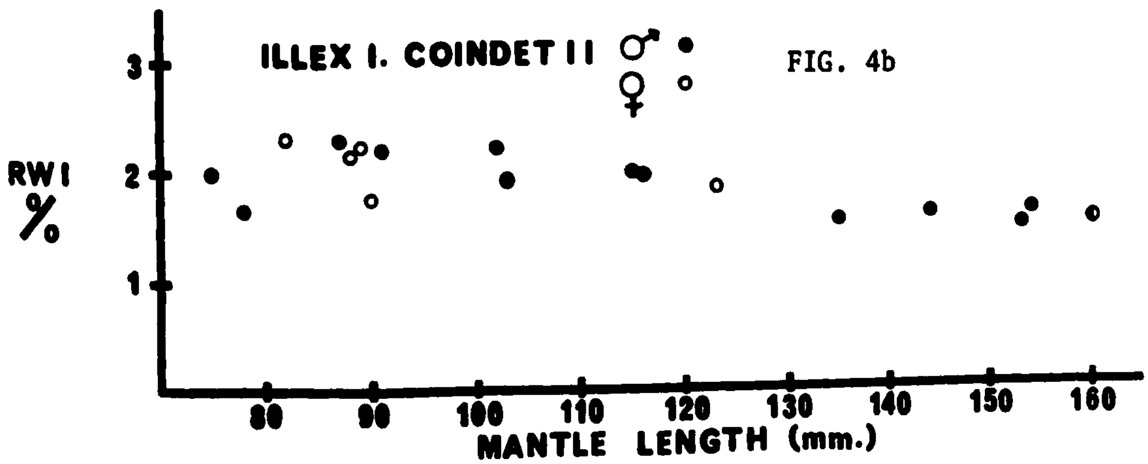


FIG. 4b

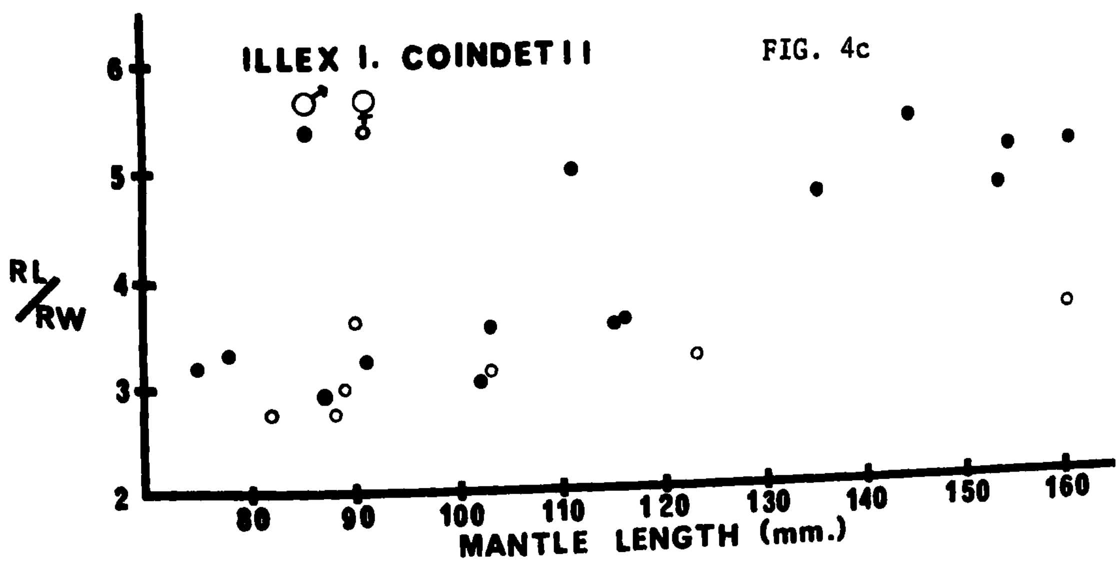


FIG. 4c

It is apparent from the data presented in these figures that *I. i. coindetii* is characterized by a longer radula than is *I. i. illecebrosus*. Furthermore, no correlation between sex and the size of the radula in terms of mantle length is apparent in *I. i. illecebrosus*, however such a correlation does exist with respect to *I. i. coindetii*.

In Plate 37, in addition to a drawing of two rows of radular teeth of *I. i. coindetii* (Figure 1), based on Naef (1923), are presented three photographs of representative portions of radular ribbons of all three subspecies. These are so similar and agree closely with information from other sources (but not all) that it is difficult to separate them on the basis of tooth structure alone. It should be pointed out that although Naef (1923) indicated marginal plates (Plate 37, Figure 1), these are not consistently present and not well developed to any extent, as can be seen in Plate 54.

Considerable attention was given to an examination in detail of radulae of *Illex*. In Figures 50, 51 and 52 are presented montage photographs of the complete radular ribbons of *I. i. illecebrosus*, *I. i. coindetii* and *I. i. argentinus*, respectively. In addition, the radular ribbon of *I. i. illecebrosus* has been considered in portions, or sections, namely, rows 1-8, 8-18, 18-30 and 30 to the terminal anterior-most row. A comparison of rows 11.5 (13) through 20 in male and female *I. i. illecebrosus* is presented in Plate 55, and for rows 11 through 20 of both male and female *I. i. coindetii* in Figure 56. All these are discussed in a separate section of this presentation under the heading "Ommastrephids".

Detailed variations within the radular of *I. i. illecebrosus*, namely, an increased number of cusps on the inner lateral teeth, and variations in the degree of spacing separating ectocones from the rachidian mesocones (Plate 58) are also discussed separately, as is the development of new teeth shown in Plate 59.

Genus *Todaropsis*

This genus (Plate 38, Figures 1 and 2) is closely related to *Illex* and a superficial examination of specimens of these two genera could easily result in confusion of identification. In the collections of *Illex illecebrosus coindetii* from the Mediterranean, one misidentified specimen was subsequently re-identified as *Todaropsis eblanae*. The radular ribbon of *T. eblanae* possesses well developed marginal plates, which are of a moderate size in relation to that of the radular teeth, whereas the members of the genus *Illex* do not. In addition to the marginal plates, *T. eblanae* possesses bicuspid lateral teeth with basal extensions which extend medially. The inner marginal teeth also are characterized by this basal configuration. The outer marginal teeth bases exhibit small extensions which appear as if they may be notched. The cusps of all the radular teeth are acute to sub-acute.

Data on the two specimens of this species are presented in Table 16.

Plate 38

Family Ommastrephidae

Fig. 1. Portion of radular ribbon of *Todaropsis eblanae* (Ball, 1841). (Drawing after Naef, 1923).

Fig. 2. Photograph of portion of radular ribbon of *Todaropsis eblanae* (Ball, 1841), showing marginal plates.

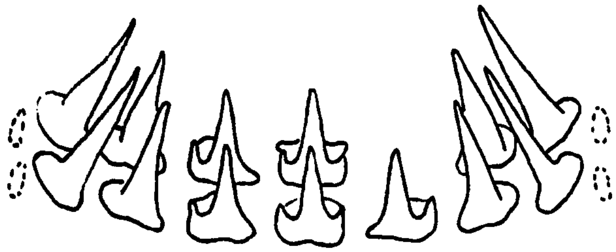


Fig. 1. *Todaropsis eblanae* (Ball, 1841). (After Naef, 1923).

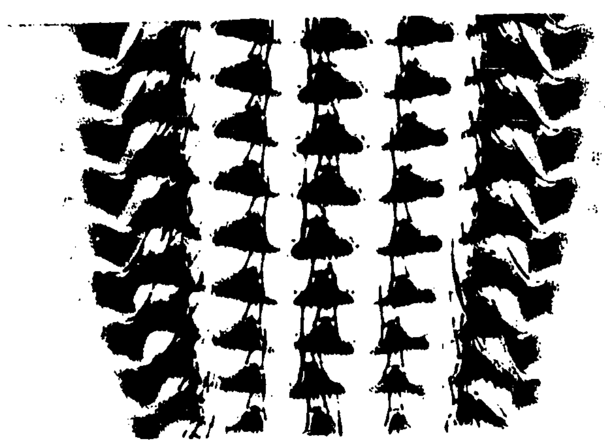


Fig. 2. *Todaropsis eblanae* (Ball, 1841).

Table 16. Mantle length, sex, buccal and radular data for *Todaropsis eblanae*.

Specimen Number	Mantle Length (mm)	Sex	Buccal Mass Diam. (mm)	Radula Length (mm)	Radula Max. Width (mm)	Radula Min. Width (mm)	Teeth No. of Horiz. Rows	Teeth No. of Longit. Rows
2*	94	F	13.5	7.3	1.7	1.5	56	7
1	125	M	15.0	12.0	3.1	1.9	55	7

*Misidentified originally as *I. i. coindetii*.

Genus *Todarodes*

Todarodes sagittatus, illustrated in Plates 39 and 40, Figure 1, displays the heterodont condition found in the other genera of this family. In Plate 39, it can be seen that the radular teeth are large and strongly cuspidate. The rachidian teeth are tricuspid with tall median mesocones and ectocones which are curved and directed toward the posterior. The lateral teeth are also tricuspid, with lateral ectocones which are moderately tall in relation to the size of these teeth, whereas the cusps on the medially directed surfaces of the basal portion of the teeth are the smaller of the ectocones. The inner marginal teeth are partially hidden by the elongate, recurved outer marginal teeth.

That there are mediad extensions of the bases of these teeth is, unfortunately, partially hidden in these photographs, due to difference in levels of focus. On these basal extensions are borne small cusps. The inner marginal teeth are therefore bicuspidate. The cusps of the radular teeth are acute to sub-acute, except where broken (Plate 39a). Marginal plates in this species are moderately small in size, but well developed. The drawing from Naef (1923) (Plate 40, Figure 1) does not agree in all particulars with the photographs in Plate 39.

Data on the two specimens of T. *sagittatus* from the Mediterranean are presented in Table 17.

Table 17. Mantle length, sex, buccal and radular data for *Todarodes sagittatus*.

				Radula			Teeth	
Specimen Number	Mantle Length (mm)	Sex	Buccal Mass Diam. (mm)	Length (mm)	Max. Width (mm)	Min. Width (mm)	No. of Horiz. Rows	No. of Longit. Rows
1	300	F	30.5	26.0	5.5	3.5	80	7
2	280	F	31.0	22.9	5.3	3.2	72	7

Genus *Ommastrephes*

Another genus of the Family Ommastrephidae represented, *Ommastrephes*, is illustrated in Plate 40 (Figures 2, 3 and 4). Here, too, the heterodont condition is evident, with tricuspid rachidian teeth, bicuspid lateral teeth, and unicuspid inner and outer marginal teeth.

Plate 39

Family Ommastrephidae

Fig. 1. Photographs of portion of radular ribbon of *Todarodes sagittatus* (Lamarck, 1799).

a. Central portion

b. Lateral portion

Fig. 1. a. *Todarodes sagittatus* (central portion)

Fig. 1. b. *Todarodes sagittatus* (lateral portion)

Plate 40

Family Ommastrephidae

Fig. 1. Two rows of radular teeth of *Todarodes sagittatus* (Lamarck, 1799) (*Ommastrephes* (*Ommatostrephes*) *sagittatus* Lamarck, 1799). (Drawing after Naef, 1923)

Fig. 2. Teeth of left half of a row from the radular ribbon of *Ommastrephes* (*Stenoteuthis*) *pteropus* (Steenstrup, 1855). (Drawing after Verrill, 1880)

Fig. 3. Partial row of radular teeth of *Ommastrephes bartrami* (Lesueur, 1821) (=*Architeuthis megaptera* Verrill, 1879). (Drawing after Verrill, 1880)

Fig. 4. Two rows of radular teeth of *Ommastrephes bartrami* (Lesueur, 1821). (Drawing after Naef, 1923)

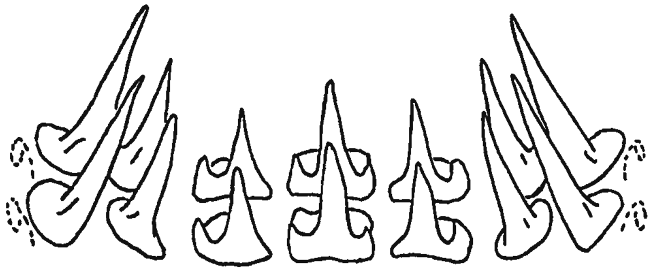


Fig. 1. *Todarodes sagittatus* (Lamarck, 1799) (*Ommastrephes* (*Ommatostrephes*) *sagittatus* Lamarck, 1799). (After Naef, 1923)

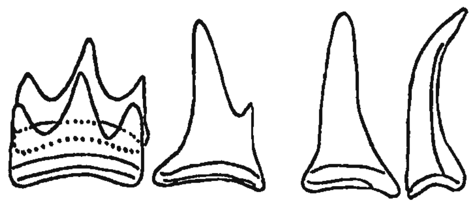


Fig. 2. *Ommastrephes* (*Stenoteuthis*) *pteropus* (Steenstrup, 1855). (After Verrill, 1880)

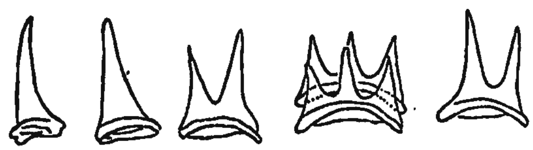


Fig. 3. *Ommastrephes bartrami* (Lesueur, 1821) (*Architeuthis megaptera* Verrill, 1879). (After Verrill, 1880)

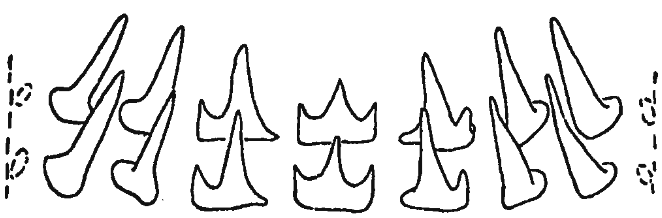


Fig. 4. *Ommastrephes bartrami* (Lesueur, 1821). (After Naef, 1923)

Ommastrephes (*Stenoteuthis*) *pteropus* (Figure 2), exhibits a lateral tooth with one large and one rather small laterally placed cusp. The radular teeth of *O. bartrami* as presented in Figures 3 and 4 are quite different and do not agree. In Figure 3 (after Verrill, 1880), the rachidian and lateral teeth are shown to possess tall cusps of approximately equal height arising from broad,shallow bases, whereas Figure 4 (after Naef, 1923), presents these teeth with cusps of unequal height arising from broad, less shallow bases. Only the outer marginal teeth of these three species show a slight degree of curvature, with *O. pteropus* (Figure 2) having the greatest degree of curvature. Marginal plates for the representatives of *Ommastrephes* are shown only in Figure 4 (*O. bartrami*, after Naef, 1923).

Genus *Ornithoteuthis*

This genus (Plate 41, Figure 2) is illustrated by a drawing of a partial row of radular teeth of *Ornithoteuthis antillarum*, from Voss (1957). The dentition shown is heterodont with the teeth bearing elongated cusps. The rachidian tooth is tricuspid with a tall mesocone and considerably smaller ectocones. The lateral tooth is seen to be bicuspid with a rounded or blunt large cusp and small acute lateral cusp. The inner marginal tooth is slender and elongate. The outer marginal tooth being slender, rather elongated and sweepingly recurved. No marginal plates are shown.

Family Thysanoteuthidae

Genus *Thysanoteuthis*

This genus is illustrated in Plate 41, Figure 1, by a portion of

Plate 41

Family Thysanoteuthidae

Fig. 1. Two rows of radular teeth of *Thysanoteuthis rhombus* Troschel, 1857. (Drawing after Naef, 1923)

Family Ommastrephidae

Fig. 2. Teeth of left half of row from the radular ribbon of *Ornithoteuthis antillarum* Adam, 1957. (Drawing after Voss, 1957)

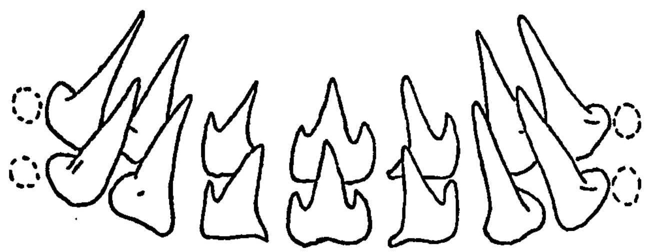


Fig. 1. *Thysanoteuthis rhombus* Troschel, 1857.
(After Naef, 1923)

Fig. 2. *Ornithoteuthis antillarum* Adam, 1957.
(After Voss, 1957)

the radular ribbon of *Thysanoteuthis rhombus*, drawn by Naef (1923). The heterodont condition is shown in the tricuspid rachidian teeth, bicuspid lateral teeth (of approximately the same height as the rachidian teeth) which also appear to possess a small medially directed extension of their bases. The inner and outer marginal teeth are taller than the others, unicuspid and not apparently recurved. The presence of marginal plates is indicated.

Family Chiroteuthidae

Genus *Chiroteuthis*

This genus is represented by two species, *C. capensis* and *C. veranyi* (Plate 42, Figures 2 and 3), which exhibit the heterodont condition. In Figure 2, the drawing of Voss (1967) of *C. capensis* shows a tricuspid rachidian tooth that is taller than the bicuspid lateral teeth and of approximately the same size as the inner marginal teeth, only one of which is shown to be bicuspid. The outer marginal teeth are taller than the other radular teeth and appear to be slightly recurved.

Chiroteuthis veranyi (Figure 3) is depicted by Naef (1923) to have a tricuspid rachidian tooth of approximately the same height as are the bicuspid lateral teeth. The rachidian ectocones are laterally directed, as are the small cusps of the lateral teeth. The unicuspid inner marginal teeth are taller than the rachidian and lateral teeth, while the unicuspid outer marginal teeth are tall, elongate and exhibit a slight degree of recurvature. Neither Figures 2 or 3 presents any indication of marginal plates for this genus.

Plate 42

Family Chiroteuthidae

Fig. 1. Single row of radular teeth of *Valbyteuthis danae* Joubin, 1931. (Drawing after Roper & Young, 1967)

Fig. 2. Single row of radular teeth of *Chiroteuthis capensis* Voss, 1967. (Drawing after Voss, 1967)

Fig. 3. Single row of radular teeth of *Chiroteuthis veranyi* (Férussac, 1835). (Drawing after Naef, 1923).

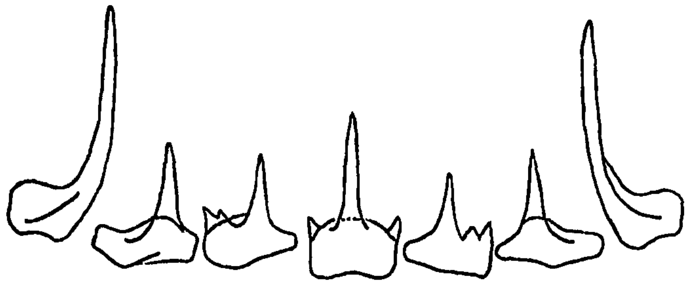


Fig. 1. *Valbyteuthis danae* Joubin, 1931.
(After Roper & Young, 1967)

Fig. 2. *Chiroteuthis capensis* Voss, 1967.
(After Voss, 1967)

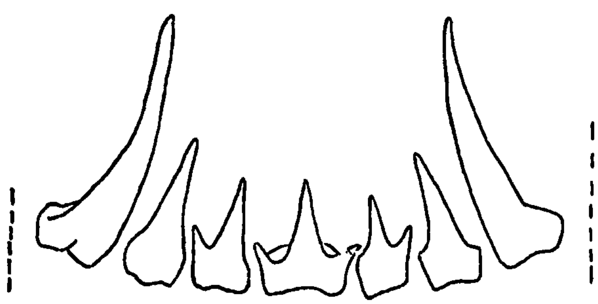


Fig. 3. *Chiroteuthis veranyi* (Férussac, 1835).
(After Naef, 1923)

Genus *Valbyteuthis*

The illustration of a single row of radular teeth of *V. danae* (Plate 42, Figure 1), is a bit unusual. The mesocone of the rachidian tooth is slender and elongated, much taller than its lateral ectocones or the lateral and inner marginal teeth. The bases of these teeth are broad in relation to the height and slenderness of their cusps.

The lateral teeth are tricuspid in a manner not heretofore seen. In addition to the small,medially directed basal extension of the lateral teeth, there is a large lateral base extension from which two smaller acute cusps arise at its outer margin.

The inner marginal teeth are broadly based, with a lateral base extension. The outer marginal teeth are slender, elongate, not sharply recurved, and the cusp projects posteriad. No marginal plates are evident.

Family Mastigoteuthidae

Genus *Mastigoteuthis*

This family is represented by an illustration (Plate 43, Figure 2) of a single row of radular teeth of *M. cordiformis*, after Adam (1954). The tall mesocone of the tricuspid rachidian tooth rises as a moderately broad triangle from a broad base towering above the small lateral ectocones. It is taller than the bicuspid lateral teeth and is of approximately equal height to the unicuspid inner marginal teeth. These broadly triangular inner marginals appear somewhat similar in shape to corresponding teeth of certain of the loliginids. The outer marginal

Plate 43

Family Promachoteuthidae

Fig. 1. Single row of radular teeth of *Promachoteuthis* sp. (Drawing after Roper & Young, 1968)

Family Mastigoteuthidae

Fig. 2. Single row of radular teeth of *Mastigoteuthis cordiformis* Chun, 1908. (Drawing after Adam, 1954)

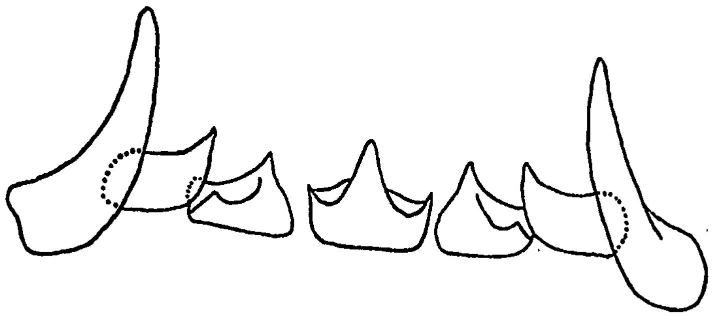


Fig. 1. *Promachoteuthis* sp.
(After Roper & Young, 1968)

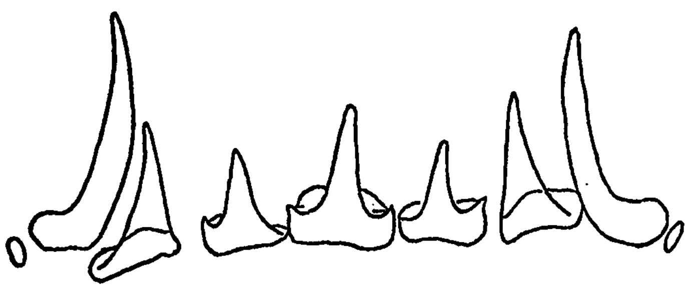


Fig. 2. *Mastigoteuthis cordiformis* Chun, 1908.
(After Adam, 1954)

teeth show a distinct angle of recurvature close to their bases whereas in other species these teeth are recurved along their length. Small marginal plates are present.

Family Promachoteuthidae

Genus *Promachoteuthis*

The illustration of the radular teeth of an unidentified promachoteuthid (Plate 43, Figure 1), shows a certain resemblance to the radular teeth of *Gonatus fabricii* (Plate 26, Figure 1) in that the lateral and inner marginal teeth of *Promachoteuthis* sp. share the laterally elongated bases and the squat, unicuspid shape of the lateral teeth of *G. fabricii*. In Figure 1 (Plate 43) the lateral teeth show a line which may represent either a small cusp or a sculptured portion of the tooth's surface. The tricuspid rachidian tooth is broad based and its mesocone is short and broadly triangular. The ectocones are short, acute and laterally directed. The outer marginal teeth are stout and gradually recurved in a medially posterior direction. No marginal plates are indicated.

Family Cranchiidae

Genus *Pyrgopsis*

The Family Cranchiidae is represented here by four genera (Plates 44 and 45). *Pyrgopsis pacifica* (Plate 44, Figure 1) exhibits heterodont dentition. The tricuspid rachidian tooth is large, broader based, with a mesocone that is taller than the bicuspid lateral and unicuspid inner marginal teeth. The ectocones of the rachidian tooth are short and broad in configuration. The lateral teeth show a large, broadly triangular cusp and a short, broad lateral cusp. The cusps of the inner marginal teeth are broadly triangular. The outer marginals are elongated, taller than the other radular teeth and slightly recurved. Small marginal plates are present.

Genus *Verrilliteuthis*

The illustration (Plate 44, Figure 2) of *V. hyperborea* from Verrill (1880) shows rather broad based teeth, rather squat in appearance. The tricuspid rachidian tooth displays a tall, broad mesocone and short, laterally directed ectocones. The lateral teeth show a large, triangular cusp and a smaller, laterally directed cusp, arising from a broad base. The inner marginal teeth are partially hidden by the recurved outer marginal teeth, but show a stout cusp. Moderately large marginal plates are present.

Genus *Phasmatopsis*

The single row of heterodont radular teeth of *P. cymoctopus* shown here (Plate 45, Figure 1), appear to be almost indefinite in shape. The tooth bases are broad, rather rounded and the cusps appear to rise in a vaguely triangular shape. The tricuspid rachidian exhibits a broad, blunt mesocone and rather small laterally oriented ectocones. The bicuspid lateral teeth have a large medially inclined cusp and a small laterally located cusp which is laterally directed. The unicuspid inner marginal teeth show a sharp medial curvature, as do the taller, bluntly unicuspid outer marginal teeth, but the degree of curvature of these latter teeth is not as great. Marginal plates are not indicated.

Plate 44

Family Cranchiidae

Fig. 1. Single row of radular teeth of *Pyrgopsis pacifica* (Issel, 1908). (Drawing after Voss, 1967)

Fig. 2. Portion of radular ribbon of *Verrilliteuthis hyperborea* (Steenstrup, 1856) (*Desmoteuthis tenera* Verrill, 1880). (Drawing after Verrill, 1880)

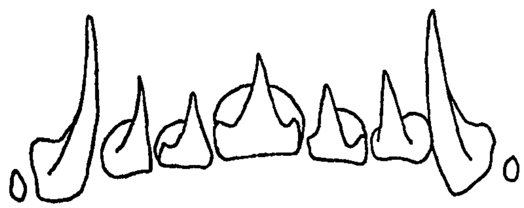


Fig. 1. *Pyrgopsis pacifica* (Issel, 1908). (After Voss, 1967)

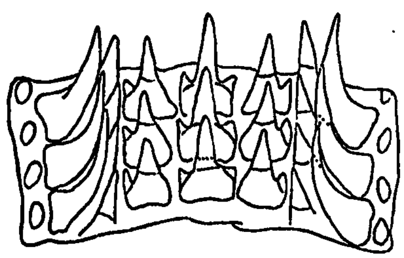


Fig. 2. *Verrilliteuthis hyperborea* (Steenstrup, 1856) (*Desmoteuthis tenera* Verrill, 1880). (After Verrill, 1880)

Plate 45

Family Cranchiidae

Fig. 1. Single row of radular teeth of *Phasmatopsis cymoctypus* de Rochebrune, 1884. (Drawing after Clarke, 1962b)

Fig. 2. Single row of radular teeth of *Megalocranchia megalops australis* Voss, 1967. (Drawing after Voss, 1967)

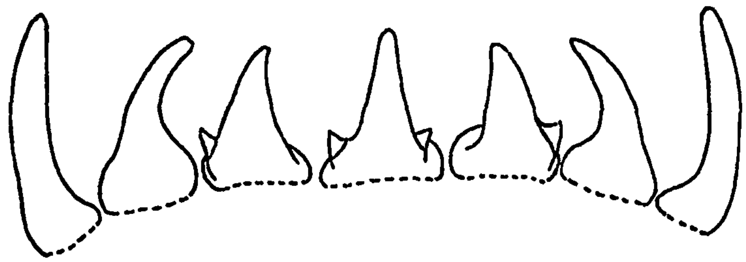


Fig. 1. *Phasmatopsis cymoctypus* de Rochebrune, 1884. (After Clarke, 1962b)

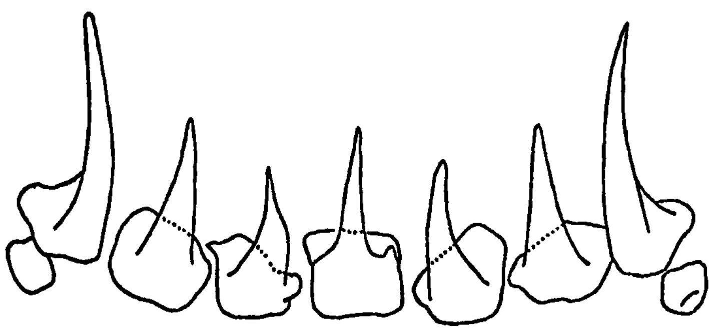


Fig. 2. *Megalocranchia megalops australis* Voss, 1967. (After Voss, 1967)

Genus *Megalocranchia*

The heterodont radular teeth of *M. megalops australis* (Plate 45, Figure 2), present a very different appearance from those of *Phasmatopsis cymoctypus*. In the former, the cusps are elongate, slender, acute to sub-acute, with the rachidian tooth exhibiting a peculiar bicuspidate condition, that is, a single small and blunt ectocone is located to one side of the tall mesocone. One of the lateral teeth shows a sharply attentuated large cusp and a lower "lump", which may or may not be a cusp or extension near the medial margin of the base. Both of the lateral teeth, as well as the unicuspid, triangular shaped inner marginal teeth, show a degree of mediad curvature (or inclination), but to a greater extent in the laterals. The unicuspid outer marginal teeth are elongate, tall and curved along their entire length. The marginal plates are large and appear to be well developed.

Order Octopoda

Family Octopodidae

Genera *Octopus*, *Bathypolypus* and *Pteroctopus*

Representative genera of the Family Octopodidae are here illustrated in Plates 46 and 47 (Figure 1). These, namely, *Octopus vulgaris*, *O. fujitai*, *O. bairdii*, *O. saluti*, *Bathypolypus sponsalis* and *Pteroctopus tetracirrhus*, have certain features in common with respect to the radula. These are: well developed marginal plates, large and well developed rachidian teeth, small or reduced lateral teeth, and well developed outer marginal teeth. In Plate 46 (Figure 1), *O. vulgaris*

Plate 46

Family Octopodidae

Fig. 1. Single row of radular teeth, plus the rachidian tooth of a second row, of *Octopus vulgaris* Lamarck, 1798. (Drawing after Adam, 1954)

Fig. 2. Portion of radular ribbon of *Octopus* (*Polypus*) *fujitai* (Sasaki, 1929). (Drawing after Sasaki, 1929.)

Fig. 3. Portion of radular ribbon of *Octopus bairdii* Verrill, 1880. (Drawing after Verrill, 1880)

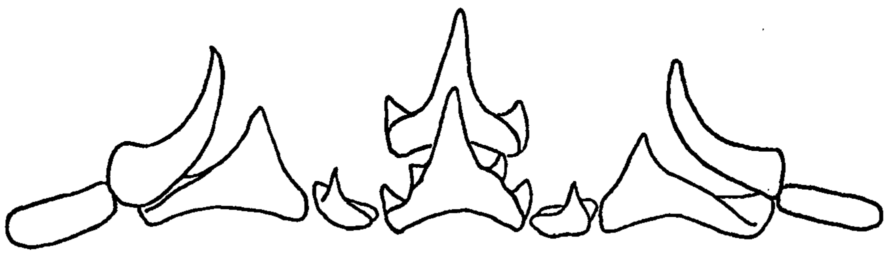


Fig. 1. *Octopus vulgaris* Lamarck, 1798.
(After Adam, 1954)

Fig. 2. *Octopus (Polypus) fujitai* (Sasaki, 1929). (After Sasaki, 1929)

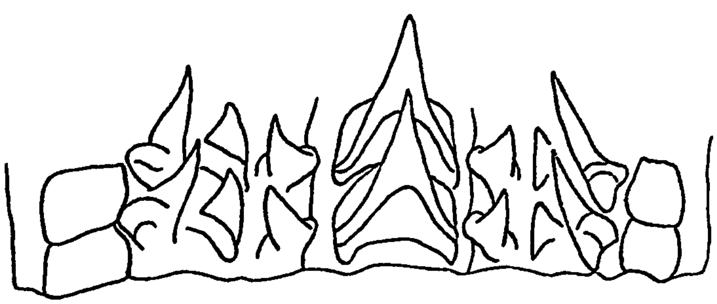


Fig. 3. *Octopus bairdii* Verrill, 1880.
(After Verrill, 1880)

Plate 47

Family Octopodidae

Fig. 1. Photograph of portion of radular ribbon of *Octopus saluti* Verany, 1839.

Fig. 2. Photograph of portion of radular ribbon of *Pteroctopus tetracirrhus* (Delle Chiaje, 1830).

Fig. 3. Photograph of portion of radular ribbon of *Bathypolypus sponsalis* Robson, 1921.

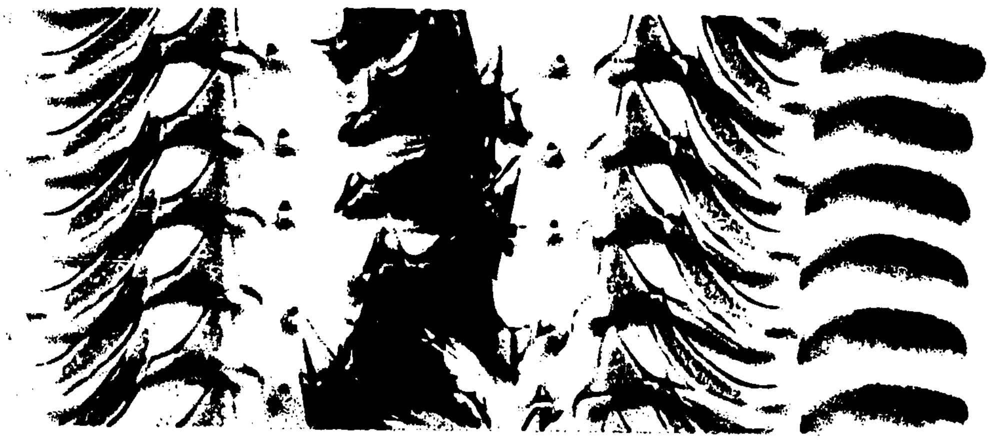


Fig. 1. *Octopus salutii* Verany, 1839.

Fig. 2. *Bathypolypus sponsalis* Robson, 1921.

Fig. 3. *Pteroctopus tetracirrhus* (Delle Chiaje, 1830).

Plate 48

Family Argonautidae

Fig. 1. Teeth from the left half of the radular ribbon of *Argonauta argo* Linné, 1758. (Drawing after Sasaki, 1929)

Fig. 2. Single row of radular teeth of *Argonauta hians* Solander, 1786. (Drawing after Adam, 1954)

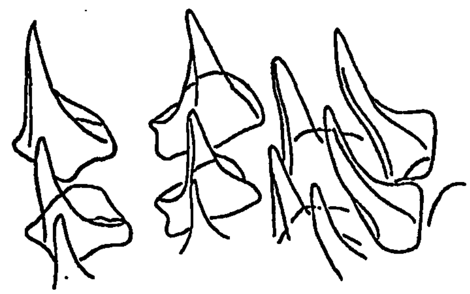


Fig. 1. *Argonauta argo* Linné, 1758.
(After Sasaki, 1929)

Fig. 2. *Argonauta hians* Solander, 1786
(After Adam, 1954)

Plate 49

Family Ocythoidae.

Fig. 1. Teeth from the right half of a row from the radular ribbon of *Ocythoë tuberculata* Rafinesque, 1814, based on figures of Brock & Jatta. (Drawing after Robson, 1932)

Fig. 2. Teeth from the right half of a row from the radular ribbon of *Ocythoë tuberculata* Rafinesque, 1814. (Drawing after Robson, 1932)

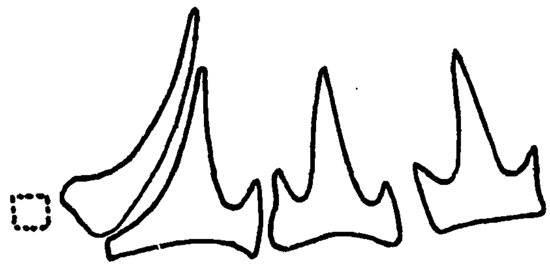


Fig. 1. *Ocythoë tuberculata* Rafinesque, 1814. (Based on figures of Brock & Jatta). (After Robson, 1932)

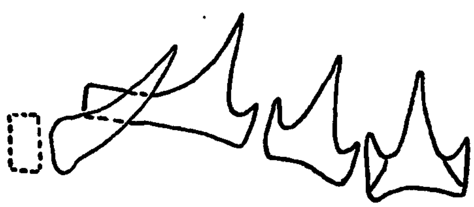


Fig. 2. *Ocythoë tuberculata* Rafinesque, 1814. (After Robson, 1932)

shows all these features plus the laterally elongated bases of the inner marginal teeth. The outer marginal teeth are tapered distally, whereas those of *O. saluti* (Plate 47, Figure 1), *B. sponsalis* (Plate 49, Figure 2), and *P. tetracirrhus* (Plate 47, Figure 3), appear to be relatively uniform in shape from base to rounded cusp, curving toward the posterior end of the radular ribbon.

The rachidian teeth of the octopods, *O. vulgaris*, *O. saluti* and *P. tetracirrhus* are equipped with variably located ectocones. However, the rachidian teeth of *O. fujitai*, *O. bairdii* and *B. sponsalis* are unicuspidate.

Family Argonautidae

Genus *Argonauta*

The illustrations of two species of the genus *Argonauta*, *A. argo* and *A. hians*, (Plate 48, Figures 1 and 2) show certain features in common. Generally the teeth are broad based and appear triangular in shape, except for the rachidian tooth of *A. hians* which is shown to be tricuspid. In addition, the lateral teeth of *A. hians* seem to differ with respect to cusp height, while the inner and outer marginal teeth appear to be of equal height. The radular teeth of *A. argo* are homodont and seem to be of the same height. Marginal plates are shown in *A. hians* to be large and well developed but barely suggested in *A. argo*.

Family Ocythoidae

Genus *Ocythoë*

In Plate 49 are presented two drawings of *O. tuberculata*. Both figures show a heterodont condition, with tricuspid rachidian and lateral teeth, bicuspid inner marginal teeth and unicuspid outer marginal teeth. However, in Figure 1, (after Brock & Jatta, from Robson, 1932), the inner lateral tooth is shown with a less laterally elongated base and the outer marginal tooth is shown to be quite elongated and curved along its length. Figure 2 (after Robson, 1932), presents the inner marginal tooth as having a greatly elongated lateral basal extension and with outer marginal tooth not as elongated or curved as is the case in Figure 1. It is also true that the marginal plates are presented differently. According to Brock & Jatta, they are square (Figure 1), while Robson figures them as being rectangular (Figure 2).

Plate 50

Family Ommastrephidae

Fig. 1. Montage of complete radular ribbon of specimen of *Illex illecebrosus illecebrosus*. Length of the radular ribbon: 8.2 mm.

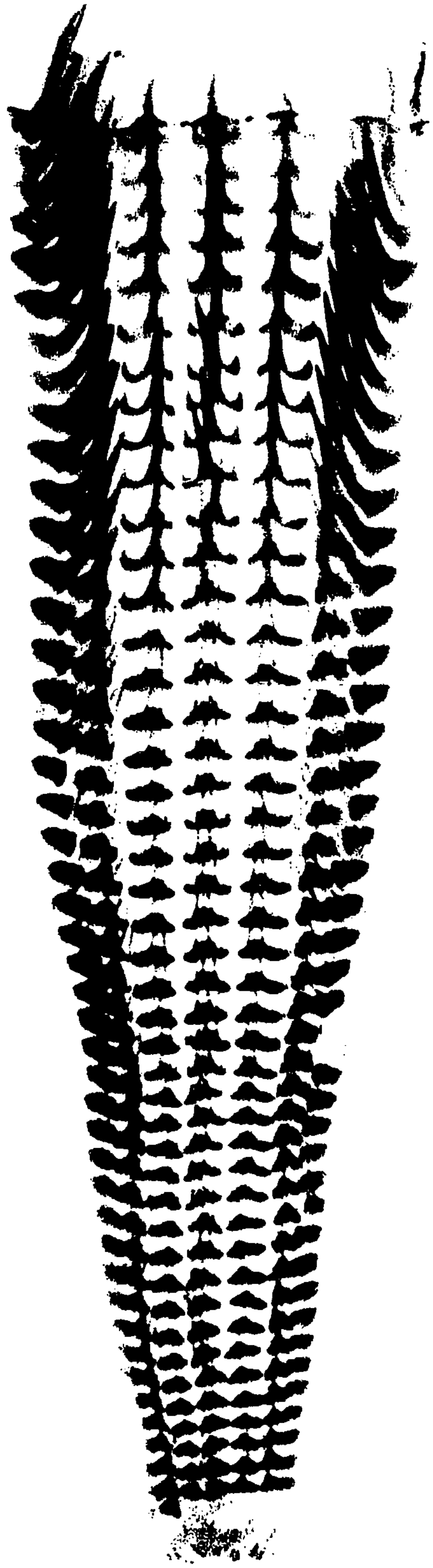


Fig. 1. *Illex illecebrosus illecebrosus.*
Complete radular ribbon.

Plate 51

Family Ommastrephidae

Fig. 1. Montage of complete radular ribbon of specimen of *Illex illecebrosus coindetii*. Length of the radular ribbon: 8.0 mm.

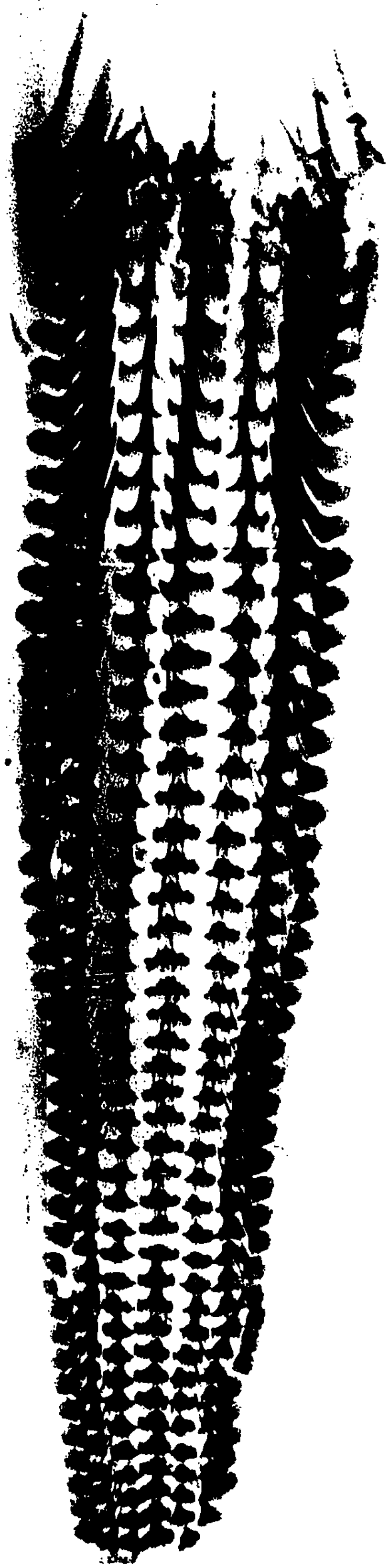


Fig. 1. *Illex illecebrosus coincetii.*
Complete radular ribbon.

Plate 52

Family Ommastrephidae

Fig. 1. Montage of complete radular ribbon of specimen of *Illex illecebrosus argentinus*. Length of the radular ribbon: 9.9 mm.

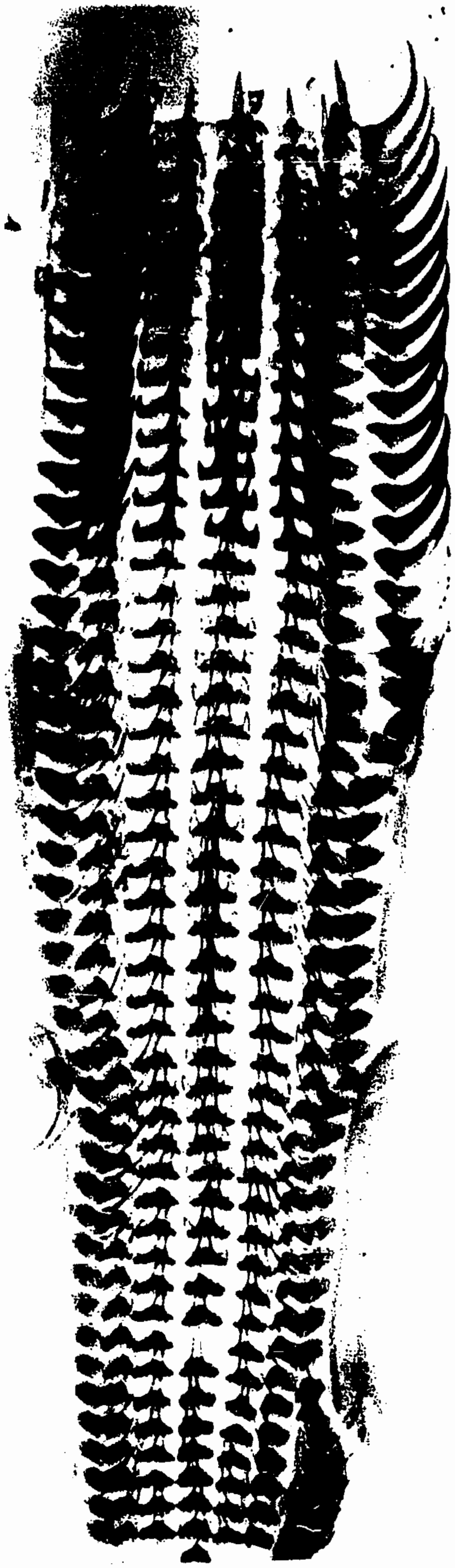


Fig. 1. *Illex illecebrosus argentinus.*
Complete radular ribbon.

Plate 53

Family Ommastrephidae

Fig. 1. Radular ribbon of specimen no. 7 of *Illex illecebrosus illecebrosus*. (Radular ribbon length: 8.2 mm).

A. Photograph of rows of radular teeth numbers 1-8.

B. Photograph of rows of radular teeth numbers 8-18.

C. Photograph of rows of radular teeth numbers 18-30.

D. Photograph of rows of radular teeth numbers 30 to the anterior end.

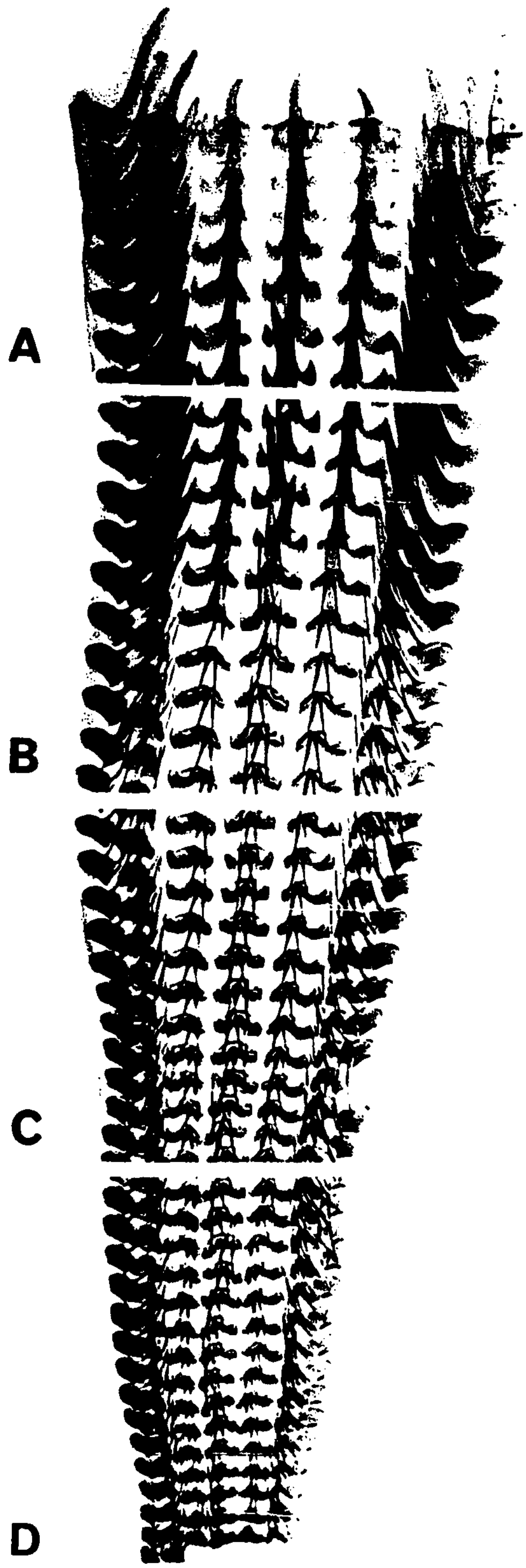


Fig. 1. *Illex illecebrosus illecebrosus*. Radular ribbon photographed in four sections, A-D.

Plate 54

Family Ommastrephidae

Fig. 1. Photograph showing marginal plates of the radular ribbon of *Illex illecebrosus illecebrosus*.

Fig. 2. Photograph showing marginal plates of the radular ribbon of *Illex illecebrosus coindetii*.

Fig. 3. Photograph showing marginal plates of the radular ribbon of *Illex illecebrosus argentinus*.

Fig. 1. *Illex illecebrosus illecebrosus*
(Marginal plates)

Fig. 2. *Illex illecebrosus coindetii*
(Marginal plates)

Fig. 3. *Illex illecebrosus argentinus*
(Marginal plates)

Plate 55

Family Ommastrephidae

Fig. 1. Photograph of rows of radular teeth numbers 11.5 through 20 from the radular ribbon of female specimen of *Illex illecebrosus illecebrosus*.

Fig. 2. Photograph of rows of radular teeth numbers 13 through 20 from the radular ribbon of male specimen of *Illex illecebrosus illecebrosus*.

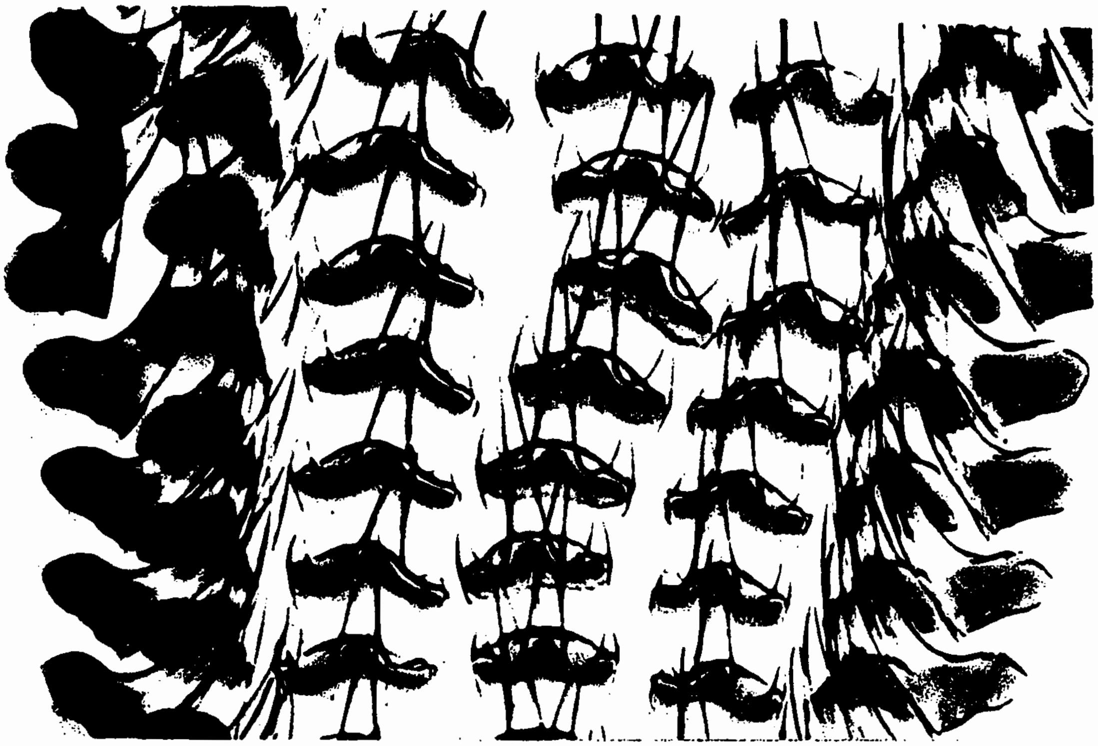


Fig. 1. *Illex illecebrosus illecebrosus* (Female)

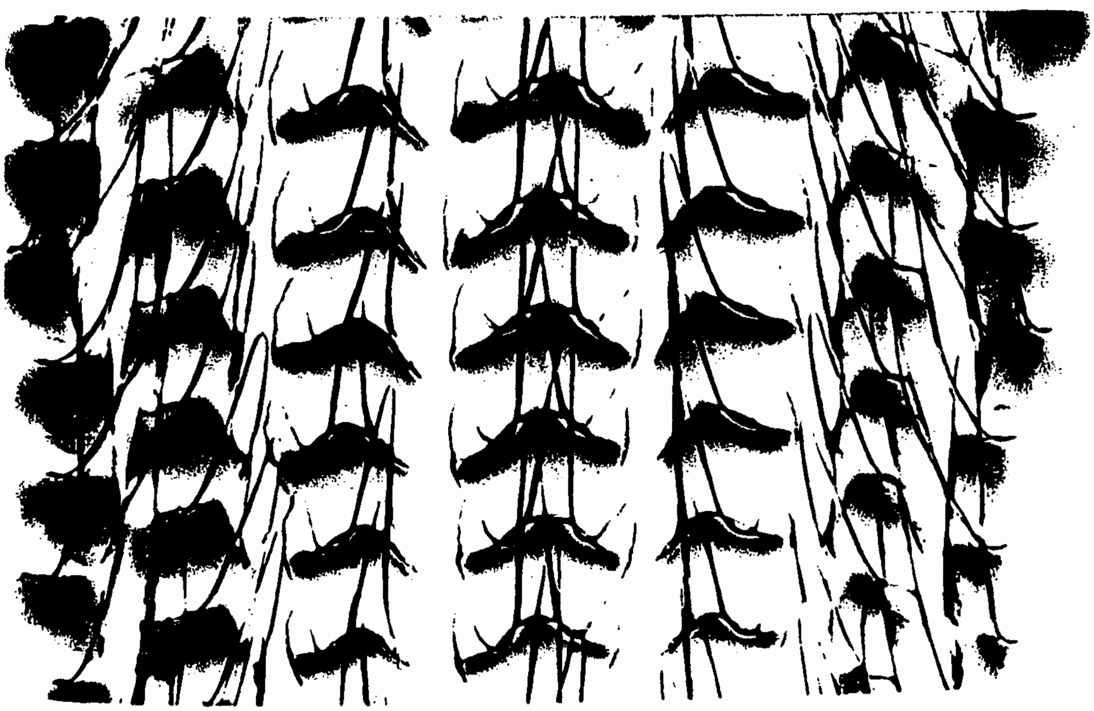


Fig. 2. *Illex illecebrosus illecebrosus* (Male)

Plate 56

Family Ommastrephidae

Fig. 1. Photograph of rows of radular teeth numbers 11 through 20 from the radular ribbon of female specimen of *Illex illecebrosus coindetii*.

Fig. 2. Photograph of rows of radular teeth numbers 11 through 20 from the radular ribbon of male specimen of *Illex illecebrosus coindetii*.

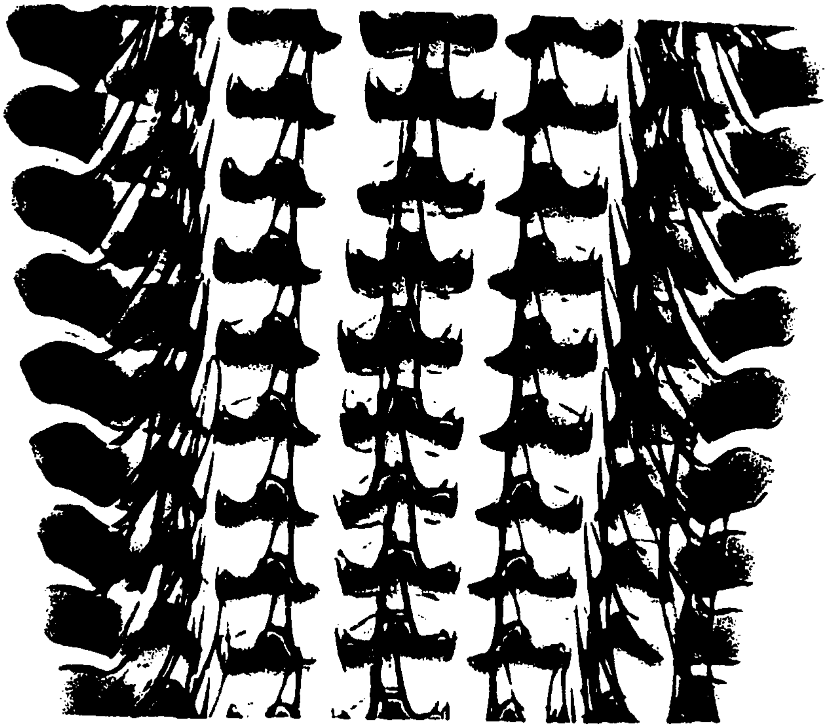


Fig. 1. *Illex illecebrosus coindetii* (Female)

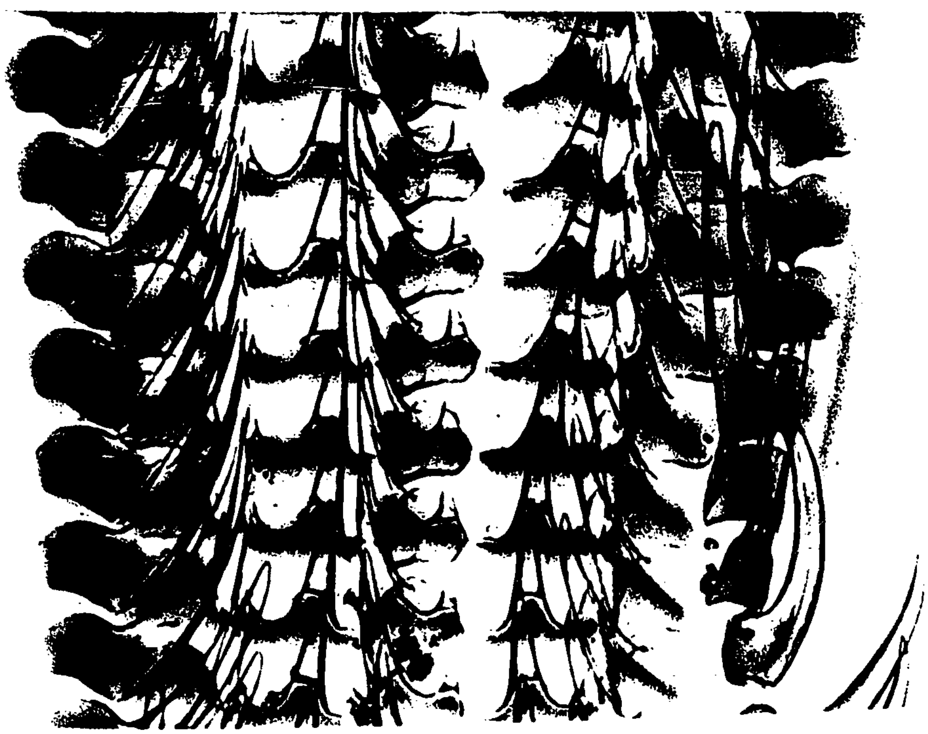


Fig. 2. *Illex illecebrosus coindetii* (Male)

Plate 57

Family Architeuthidae

Fig. 1. Photographs of rows of radular teeth from the radular ribbons from five Newfoundland specimens of the genus *Architeuthis*.

A. Lance Cove specimen (October, 1965)

B. Chapel Arm specimen (December, 1964)

C. Wild Cove specimen (November, 1966)

D. Sweet Bay specimen (November, 1966)

E. Springdale specimen (November, 1965)

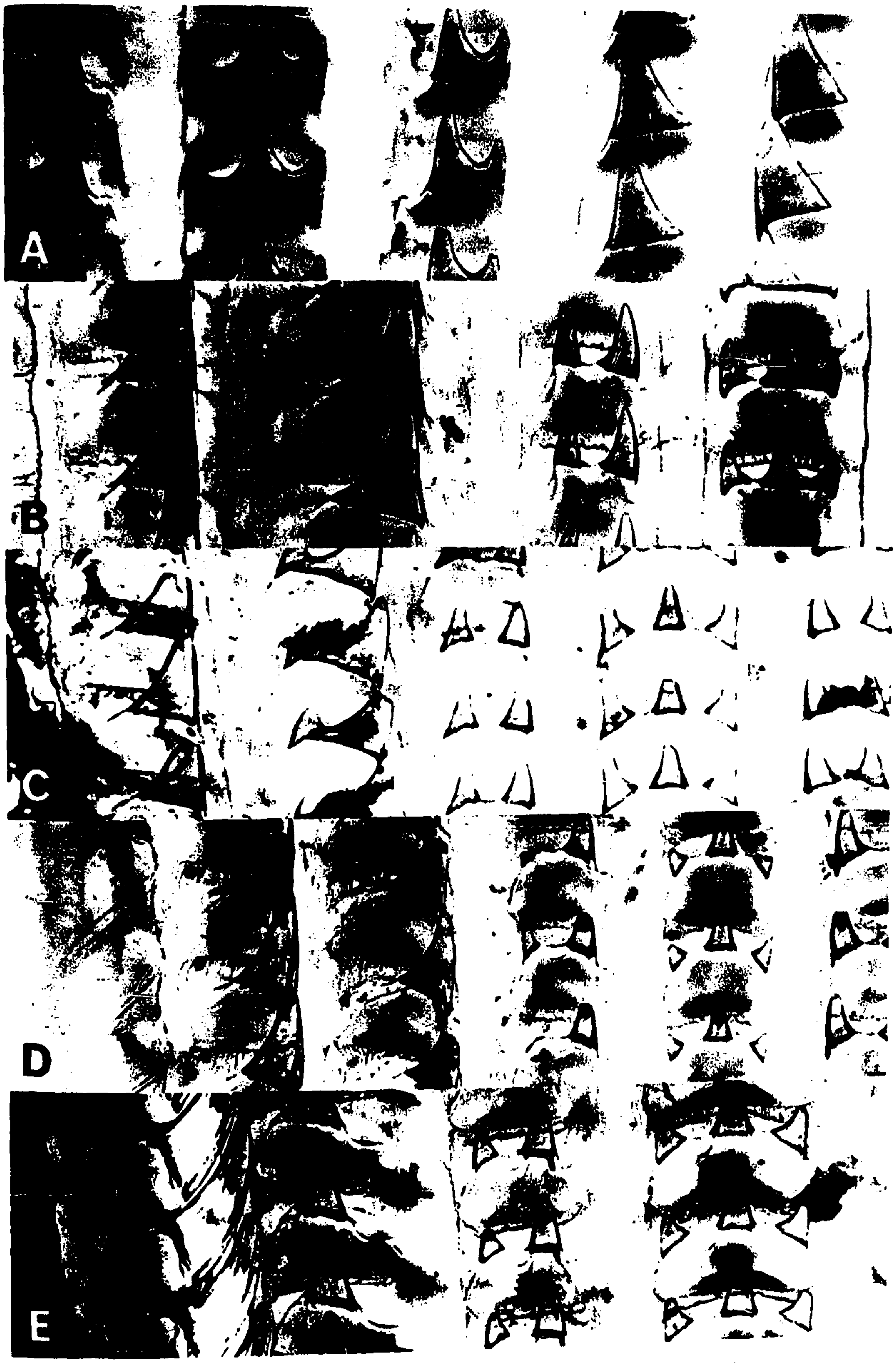


Fig. 1. Portions of five radular ribbons of specimens of the genus *Architeuthis*.

Plate 58

Family Ommastrephidae

Fig. 1. Photograph of portion of radular ribbon of specimen of *Illex illecebrosus illecebrosus* showing three-cusped inner lateral teeth.

Fig. 2. Photograph of portion of radular ribbon of specimen of *Illex illecebrosus illecebrosus* showing broadly-spaced ectocones or lateral cusps of rachidian teeth.

Fig. 3. Photograph of portion of radular ribbon of specimen of *Illex illecebrosus illecebrosus* showing narrowly-spaced ectocones or lateral cusps of rachidian teeth.

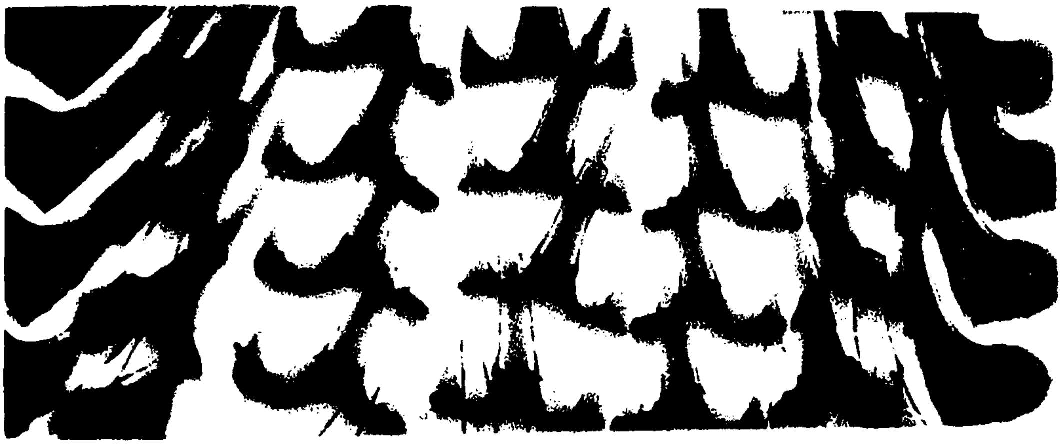


Fig. 1. Tricusped lateral teeth.

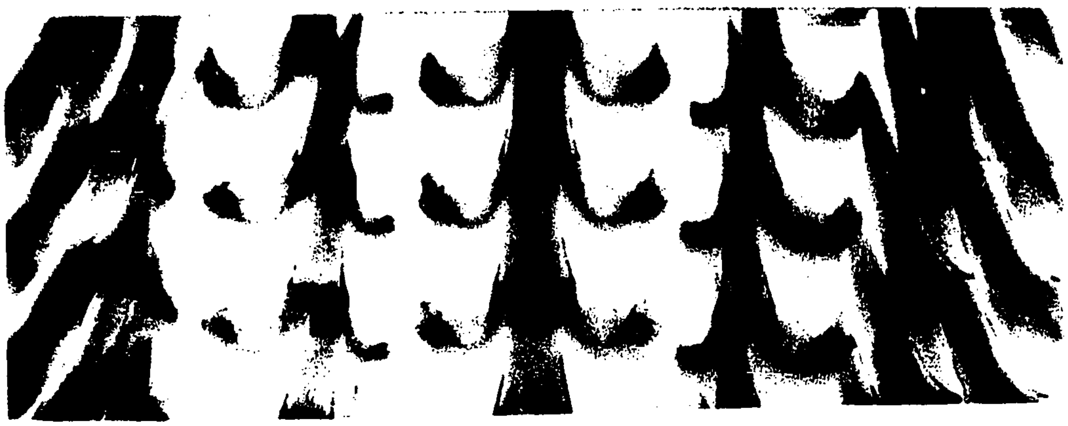


Fig. 2. Broadly spaced ectocones of rachidian teeth.

Fig. 3. Narrowly spaced ectocones of rachidian teeth.

Illex illecebrosus illecebrosus

Plate 59

Family Ommastrephidae

Fig. 1. Photograph of posterior portion of the radular ribbon of *Illex illecebrosus illecebrosus*, showing newly developing teeth.

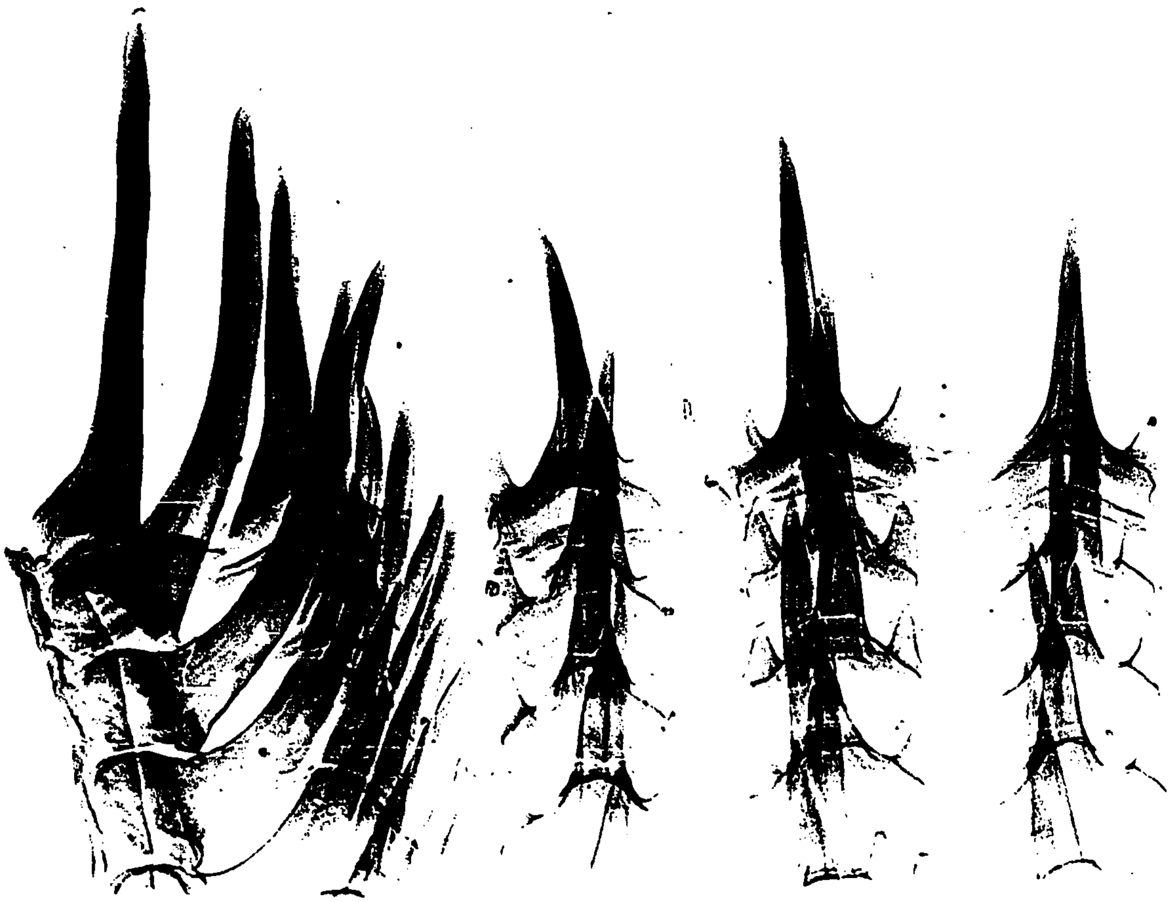


Fig. 1. *Illex illecebrosus illecebrosus.* Newly developing teeth at posterior end of radular ribbon.

DISCUSSION

Very little work has been done in the past regarding the cephalopod radula. Since Swammerdam's initial description in 1737 (Sollas, 1907) of the radula of a gastropod and Osler's confirmation of Swammerdam's work in 1832 (Sollas, 1907), work on the radula of molluscs has been done intermittently. The gastropod radula appears to have been studied extensively and its importance as a taxonomic aid has been documented elsewhere.

With reference to the radula of cephalopods, the radular teeth have been figured by many workers but there seems to have been no attempts to differentiate species or families or to use this information to any degree in taxonomy. Naef (1923) illustrated radular teeth from a variety of species, but upon comparing his drawings with the actual species, where possible, a great many inaccuracies are noticed. This situation also exists in Verrill (1880) and Sasaki (1929). Whether these inaccuracies are due to faulty observation on the part of the investigator or the artist, where one was used, is, of course, open to speculation. However, if drawings are to be used, great accuracy must be the main consideration, or the drawings are virtually worthless. Of the more recent workers, Adam's work (1934, 1952, 1954) shows the most accurate representations of radular teeth. Judging from the magnification and details shown, although it has not been stated anywhere, it appears that a camera lucida has been used. Roper (1963, 1964, 1965, 1968) seems to have used the services of an artist. Whereas the drawings are rather artistic, too often they have had to be reduced for purposes of publication and many details are completely lost or obscured and he failed to indicate any magnification.

But is it obligatory to draw these radular teeth? The answer to this varies greatly, according to the situation encountered. Photographs can be quite complete but not always so. If the teeth are not extremely tall, do not overlap greatly - and with the marginal teeth, unfortunately they do - then photographs are possible and even desirable. However, where the differences in focal levels are too great to encompass all the details in one photograph, then drawings, preferably by camera lucida, are greatly to be desired. Any character to be used as a taxonomic criterion must be accurately described and illustrated, or else its value is greatly diminished.

When the work for this thesis was started, it was considered that perhaps it would have a negative value, i.e. no great differences in radular teeth would be apparent. However, as the literature was searched, illustrations assembled and radular ribbons of specimens examined, it became abundantly clear that differences existed between genera and even species of Coleoids.

The most outstanding of these differences were found during the examination of radular ribbons of specimens collected from various areas of the world. In a group of 22 *I. i. coindetii* from the Mediterranean, the radular ribbons were quite similar except for one specimen. It did not agree with the others in the sample in that the radular ribbon showed well developed marginal plates along both sides of the radular ribbon for its entire length. The specimens were re-examined, and upon examination of such diagnostic characters as the sucker dentition, it was found that the specimen in question was not *I. i. coindetii* but *Todaropsis eblanae*. These two squid are superficially similar but by counting the number of rows of suckers on the tentacular clubs and examining the pattern of denticles within suckers, they can be separated. Here the misidentification had been "caught" initially by examination of the radular ribbon. Another misidentification occurred in the collection of *Lolliguncula brevis* from Delaware Bay. Again one radular ribbon did not "agree" with the others. The marginal plates were round and well developed, whereas all the other specimens showed curved and elongated marginal plates. A re-examination of the specimen showed that the collection included one young, sexually immature specimen of the closely related loliginid, *Loligo pealei*. It was very easy to see where the mistake had been made. The young *L. pealei* did not yet show the characteristic fin configuration and it was the same size as the specimens of *Lolliguncula brevis* that comprised the sample. Only a close examination of the small differences corrected the misidentification, pointed out again by the difference in the radular ribbon.

The Marine Sciences Research Laboratory was the recipient of a collection of an antarctic species of squid, *Bathyteuthis* sp. Upon examination of illustrations of radular teeth of two species and the radular teeth of the specimens at hand, no definite identification could be made. The genus *Bathyteuthis* consists of three species, and since I had been able to obtain information on the radular apparatus of two of these, it was not possible to arrive at a final identification on the basis of radula alone. The radular teeth of *Bathyteuthis* sp. (Plate 34, Figure 3) looked very much like those of one species illustrated by Roper (1968), but the marginal plates more closely resembled those of the other species. The answer to the problem has just been received via personal communication from Dr. Roper; the specimen was *Bathyteuthis abyssicola*, the third species of the genus - justification for the hesitancy in making an identification not truly warranted on the basis of incomplete information with respect to the radula.

The assembled illustrations of radular teeth, particularly those of Adam (1934, 1952, 1954), Voss (1956, 1957, 1962) and Roper (1964, 1966, 1967, 1968) show definite species differences. I have been at a loss to account for the lack of attention given to these differences before now. In the Family Loliginidae, (Plate 17, Figures 1, 2, 3), showing the radular teeth of three species of the genus *Doryteuthis*, the size and shape of the teeth are sufficiently different between the species, that no difficulty should be encountered in identifying members of this genus. Again in Plate 21 (Figures 1 and 2) the species of *Enoploteuthis* are so different, species identification would be greatly facilitated by examination of radular teeth. In addition, members of the genera *Gonatus* (Plate 26), *Calliteuthis* (Plates 32 and 33), *Chiroteuthis* (Plate 42) and *Rossia* (Plates 10 and 11) illustrated herein, all show definite species differences.

Not only can interspecific differences be seen by examining radular teeth, but an examination of the plates illustrating the Family Sepiidae (Plates 8 and 9), the Family Sepiolidae (Plates 11 to 14) and the Family Loliginidae (Plates 15 to 20), taking into account any artistic inaccuracies, the intergeneric differences become quite apparent.

In commenting on *Enoploteuthis cookii* Owen, Verrill (1880) observed "it is to be regretted that Professor Owen has neither described nor figured the teeth of the radula, in a manner to enable it to be used as a systematic character". I can only agree with this remark, for the radular configuration should be a regular part of the description of any new species of cephalopod. Unfortunately, Verrill (1879) presented a series of illustrations of the radula of his species *Enoploteuthis hartingii* that are not of great value in interpretion of the species, as it were, not following the dictum he quoted concerning Owen's earlier "failure". All radular drawings, if presented with the care and attention to detail characteristic of the illustrations from Adam (1954), would be of great taxonomic assistance. In the same vein, Ishikawa (1924) asked that attention be given the statocysts in description of species.

Robson (1929a, 1932) was of the opinion that the radula was of greatest importance in distinguishing higher taxonomic levels, assigning little taxonomic value to the use of radulae for the separation of species, with the possible exception of the lateral teeth (1929a). Like opinion was held by Lehmann (1967), who stated that the radula could be used for "gross taxonomic purposes - not fine points", since the radula, functioning in the swallowing of food, was "less subject to selective pressures".

I cannot agree with this, however. A species is the sum total of a great number of characteristics, of which but a few have either been used in species description or yield themselves to ready observation or measurement.

One of the foremost students of cephalopod evolution, O. H. Schindewolf (1934) was of the opinion that "all available characters of the organisms must, of course, be used as a basis for classification and phylogenetic significance, but they are of different ranks. As to their classificatory and phylogenetic significance, there is a hierarchy of characters resembling that in the scale of classification. Each differential diagnosis of the successive systematic units can be based therefore only on a single or on a few decisive characters selected from the mass of all those available. In general, the most important are considered to be the <u>internal</u>, often minute, characters and their developmental features, because they are more independent of the mode of life than the external ones".

Such "internal . . . minute characters" would be those of the radular apparatus. As already noted, I have used knowledge of the radular configuration of a given species to separate specimens of doubtful identification, but this can only be done if the knowledge of the radula, its teeth and dimensions, is known.

With regard to functional morphology, Robson (1929a) distinguished between carnivorous (octopod) and non-carnivorous (decapod) radulae. He claimed that the former type is distinguished by additional ectocones to either side of the mesocone of the rachidian tooth and by a greater differentiation in individual tooth-types. Be that as it may, squids are definitely carnivorous. As noted earlier, there is little agreement on the role played by the radular apparatus in the feeding process. That the radula is used is almost certain, since the wearing away of the cusps from the newly-formed condition seen in Plate 59 is readily evident. In Plate 53 the progress deterioration of the cusps can be seen by comparing the teeth in Section D (Rows 30 to the anterior end) and those of Sections A, B and C. If the radula is an aid in swallowing similar to the roughened cat's tongue, as suggested by Bidder (1950, 1966), this action would be brought to bear in the more anterior portion of Section C, and all of Section D, the areas showing the greatest wear on the cusps. Also, it should be pointed out that the teeth are situated on the ribbon so that when the radula is moved in an anteriad direction the cusps do not impede this movement. Since the radula is curved over a muscular projection in the floor of the mouth (Plates 1, 4, 6 and 7), with the area of greatest curvature falling in the anteriormost portions of Section C. This position (i.e., the curvature) would result in the teeth being pitched in such a way as to "fork" food material and pass it along posteriorally during swallowing or passage from the buccal mass into the esophagus as the radula is moved posteriad. The word "radula" is derived from the Latin radere, meaning to scrape. Such a designation applies equally well to both the "cat's tongue" function and to the more widely understood function of rasping in other molluscan classes. As noted earlier, this "cat's tongue" action agrees with the short period of ingestion, disfavouring rasping activity. Finally, Berry (1928) speculated that the mandibles and the relatively narrow oral aperture were important evolutionary adaptations in the pelagic mode of life of modern decapods. Berry should have included the radula and what I believe to be its primary role - that of an aid to swallowing (and thereby fostering retention of food pieces excised by the beak - as being of equal evolutionary importance.

Architeuthids

The Family Architeuthidae, however, presents a few problems. Not only are these large specimens few in number, but it has been only since Verrill's work in 1879 that any orderly examination of these few has taken place, despite the pioneer studies of Steenstrup (1857). It is indeed unfortunate that those examined have been obtained after the animals have been washed ashore or found floating on the ocean's surface in a dead or dying condition, usually in an area not readily accessible to scientific investigators. Too often the specimen's condition is too poor due to battering by wave action and decay, to allow any extensive morphological examination. The soft-bodied nature of the architeuthids limits the number of hard parts, e.g., sucker rings, gladius, mandibles and radula, available for examination. Considering the radular teeth illustrated in Plates 28-30 and Plate 57, the number of species represented becomes slightly confusing. Again, taking into account artistic liberties and liabilities, we must consider the differences in teeth shown from various locations on the radular ribbon (Plate 28, Figure 2 a and b; Plate 29, Figure 2 a and b). Radular teeth on the anteriormost portion of the radular ribbon are smaller, often broken and show signs of wear (blunted or rounded tooth cusps). Those teeth on the posteriormost portion of the radular ribbon (enclosed in the radular sac) or the area of odontogenesis (Plate 59, Figure 1), are not yet completely formed. However, the teeth more anterior or somewhat removed from the area of odontogenesis and region of tooth development, but still enclosed within the radular sac are probably the best to use for diagnostic purposes. This is the problem with all the architeuthid illustrations in that the drawings indicate no definite location. When preparing the architeuthid radulae for photography, only two complete specimens were available and these were extremely difficult to handle and clean due to their long immersion in alcohol. The radular ribbons were so thick and brittle that great care had to be taken to prevent splitting and loss of teeth, even then I was not completely successful or satisfied with the results.

Putting aside illustration inequalities, we shall examine what can be said about the radular teeth differences of the architeuthids illustrated here. The radular teeth of *Architeuthis harveyi* (Plate 28, Figures 1 and 2) closely resemble those of the architeuthid specimen from Lance Cove (Plate 57, A). The radular teeth of *Architeuthis* sp. (Plate 28, Figure 3), after Frost (1934) seem to resemble those of the Chapel Arm specimen (Plate 57, B) and those of the Sweet Bay specimen (Plate 57, D), but do not show any appreciable similarity to those of *A. harveyi* (Plate 28, Figures 1 and 2). The illustrations of teeth from Frost's (1935) second specimen of *Architeuthis* sp. (Plate 29, Figure 1 a and b) appear to resemble the radular teeth of the Springdale specimen (Plate 57, E) but the illustration (after Frost, 1935) shows too little detail to be of real value. It is interesting to note here that the architeuthids so far considered are all from the waters around Newfoundland.

The unidentified architeuthid of Mitsukuri and Ikeda (1895) (Plate 29, Figure 2 a and b) doesn't resemble the Newfoundland specimens as much as it does *A. physeteris* (Plate 30, Figure 1). The marginal plates differ appreciably, however, between these two specimens, or at least they are so illustrated.

The illustration of the radular teeth of A. *physeteris* (Plate 30, Figure 1) shows some similarity to the specimens from Lance Cove (Plate 57, A) and Sweet Bay (Plate 57, D). However, the slenderness of the inner and outer marginal teeth of A. *physeteris* emphasizes their dissimilarity.

Architeuthis longimanus (Plate 30, Figure 2) appears to display blunted or broken tooth cusps on the rachidian tooth and both lateral teeth. It may be the fault of the illustration, but I cannot see any great similarity between this species of Kirk (1888) and any others figured here. However, the teeth of A. *clarkei* (Plate 30, Figure 3 a and b) and those of A. *physeteris* (Plate 30, Figure 1) show some similarity between rachidian and lateral teeth. The illustration of A. *clarkei* with its extremely curved outer marginal tooth (Plate 30, Figure 3b) would apparently rule out the similarity but only if a lateral view of the outer marginal tooth of A. *physeteris* were shown to be dissimilar, and such an illustration is lacking.

The photographs of the radular teeth of recent Newfoundland specimens of architeuthids appear to confuse the situation. Whereas Aldrich (1968) and Aldrich and Aldrich (1968) considered all their specimens as A. *dux* Steenstrup 1857, the evidence from this comparative study of the configuration of the radular teeth would seem to disfavour this contention. As noted earlier, it is difficult to reconcile all specimens as having a uniform radular configuration. Aldrich (1968) based his unispecific theory on the basis of the lack of a series of diagnostic meristic characters on which the several species had been established. The failure of the characters which were used (i.e., head-mantle length ratio and caudal fin configuration) further supported his contention. However, the evidence from the radular apparatus study cannot support this interpretation of the five specimens at this time. External features of an animal species may change at a rate greater than that of hard internal structures, indicating that such characters may prove to be of more taxonomic value than are the more readily changed soft parts.

At any rate, the Newfoundland architeuthids apparently demonstrate radular types reminiscent of other local species, namely, A. *harveyi* (Lance Cove) specimen; *Architeuthis* sp. from Dildo, Trinity Bay, 1933 (Frost, 1934), (Chapel Arm and Sweet Bay specimens); *Architeuthis* sp. from Harbour Main, Conception Bay, 1935 (Frost, 1935) (Springdale specimen).

The specimen from Wild Cove (Plate 57, C) appears unique in many respects. It must be pointed out that the similarities noted here are consistently within specimens of species reported earlier from North Atlantic waters, of which four are generally agreed upon, i.e. A. *harveyi*, A. *princeps*, A. *clarkei* and A. *dux* (Stephen, 1962; Aldrich, 1968). The similarities between individual tooth-types with those of some of the other of the twelve recognized species (Stephen, 1962) have been also indicated. I feel that it should be stated here that only the procurement of more specimens in good condition and a re-examination of the radular teeth and marginal plates of the already identified architeuthids may bring some semblance of order to this situation.

The width of the rachidian teeth varied appreciably between the specimens of Newfoundland architeuthids. These measurements are listed in Table 10.

The two complete radular ribbons from architeuthids came from those from Lance Cove and Sweet Bay. The Lance Cove radula measured 59 mm in length and of the 94 rows, 14 rachidian teeth were greater than 1 mm in width. The other complete one, measuring 56 mm in length, from Sweet Bay, had no rachidian teeth measuring more than 1 mm in width.

With respect to the incomplete radular ribbons, the same was true for the specimen from Chapel Arm, in that no rachidian tooth exceeded 1 mm in width. The greatest rachidian tooth width is seen to occur in the Wild Cove specimen (1.254 mm). This specimen, although incomplete, provided a radular ribbon of 89 rows of teeth, of which 28 rachidian teeth measured over 1 mm. Consisting of only 54 rows of teeth and several of them partial rows, the incomplete ribbon from the Springdale specimen possessed 19 rachidian teeth greater than 1 mm in width. The greatest rachidian tooth width was 1.221 mm. It is considered significant that the rachidian teeth of the Wild Cove specimen (mantle length: 106.7 cm) were of the same size (width) as were those of the specimen from Springdale which was the largest (mantle length: 161.0 cm) of the five specimens.

Further, with regard to size, it is surprising to see that an individual specimen with a mantle length of 126.5 cm (Lance Cove) possesses a radular ribbon 59 mm in length and 11 mm in width. The larger of the two specimens with a complete radular ribbon (Sweet Bay) had a mantle length of 142.2 cm while the radular ribbon measured 56 mm in length and 11 mm in width. The difference in length of 3 mm cannot really be considered significant, if only due to the difficulties in handling and preparation noted earlier. These complete radular ribbons are relatively small when compared to that described by Verrill for a specimen of *A. monachus* Steenstrup of uncertain mantle length, namely, 70 mm in length and 12 mm in width (Tryon, 1879).

The measurements of mantle length and complete radular ribbon length show a ratio of 1:21.44 (Lance Cove specimen) and 1:25.39 (Sweet Bay specimen). For smaller species of squid different ratios exist. For the two specimens of *Todarodes sagittatus* (Table 17) ratios of 1:11.53 and 1:12.17 were computed. Taking data for the *I. i. illecebrosus* of greatest radular length (Tables 12 and 15) the ratio is 1:22.91 while for the specimen with the minimum mantle length a ratio of 1:24.77 applied. It is evident that the architeuthids possess a small radular apparatus in relation to their great overall size. Unfortunately, Iwai (1956) gives no information on the radula of an architeuthid he concluded was a young specimen of *A. japonica*.

As I noted earlier, the teeth of the five specimens differed in some respects, yet were similar in others. One of the more interesting and perhaps significant differences was the translucent "cap" portion of the rachidian and lateral teeth of the Lance Cove specimen, seen nowhere else nor figured by any of the earlier workers. Histological preparation of future specimens properly preserved may indicate the significance of this difference.

After all this comparison with what are we left? Are these architeuthids one species showing individual variations, or five species morphologically similar? I cannot make any definite statement to either effect on the basis of a five specimen sample, which included only two completely intact radular ribbons. The suggested similarities between these specimens from Newfoundland waters, may be significant but further study and a greater number of samples may answer the questions raised here.

Ommastrephids

The Family Ommastrephidae was exemplified in this study by representatives of five genera, of which there were six species, namely, *Illex illecebrosus illecebrosus*, *I. i. coindetii*, *I. i. argentinus*, *Todaropsis eblanae*, *Todarodes sagittatus*, *Ommastrephes bartrami*, *O. pteropus*, and *Ornithoteuthis antillarum*.

Of the ommastrephids illustrated herein, all are characterized by prominently developed tricuspid rachidian teeth, in which the mesocone is appreciably taller than are the ectocones. A striking feature of this group is the elongation characteristic of all the teeth, particularly in the unicuspidate inner and outer marginals and the major cusp of the bicuspidate laterals, as well as the mesocone of the rachidians.

The only exception to this is found in the rachidian teeth of the members of the genus *Ommastrephes*, in which the cusps of the rachidian teeth are shown by Verrill (1880) and Naef (1923) to be of a more uniform height (Plate 40, Figures 2, 3, 4). Similarly, Verrill (1880) represents the inner and outer marginals as being slightly taller than the lateral or rachidian teeth in *O. pteropus*. The drawings of Verrill and Naef referred to above represent the only striking departures from what appears to be a uniform similarity throughout the ommastrephids examined.

In general, ommastrephids are easily identifiable on the basis of their radular apparatus. *Todarodes sagittatus* is immediately identifiable by the bicuspidate state of the inner marginal teeth and well developed marginal plates. Marginal plates were uniformly present and well developed in the examined specimens of *Todaropsis* and *Todarodes*. *Todaropsis* differs from the only other genus in the Subfamily Illicinae (the genus *Illex*) in that marginal plates are consistently present in the former but only sporadically present in the latter. Apparently marginal plates are absent in *Ornithoteuthis*. Naef (1923) figures marginal plates in *O. bartrami* (Plate 40, Figure 4) while Verrill (1880) fails to indicate their presence in either *O. pteropus* or *O. bartrami* (Plate 40, Figures 2 and 3).

The Genus *Illex*

Currently, three subspecies of the monotypic genus *Illex*, are recognized (*I. i. illecebrosus*, *I. i. coindetii*, and *I. i. argentinus*). The radular teeth as mentioned previously all exhibit a striking similarity in their morphology so as to make specific determinations almost impossible. The similarities are probably best seen in Plates 55 and 56 where similar portions (specifically rows 11-20 in both male and female) are compared in *I. i. illecebrosus* and *I. i. coindetii*, respectively. Slight differences exist in the configuration of the marginal plates, where present, in the three subspecies (Plate 54). However, their sporadic occurrence eliminates their value as a taxonomic character.

There are, however, as previously stated, exhibited differences in the morphometric relationships between *I. i. illecebrosus* and *I. i. coindetii*, (Figures 1-4).

From data presented in Table 15, the ratio of radular length of mantle length was computed for specimens of *I. i. illecebrosus*, *I. i. coindetii* and *I. i. argentinus* of uniform mantle length. Ratios of 1:2.47 (for *I. i. illecebrosus*), 1:1.24 (for *I. i. coindetii*) and 1:1.66 (for *I. i. argentinus*), respectively, were computed.

It is, of course, unwise to base too much importance on a single specimen of a given form, but since these specimens were alike in size, they did afford the opportunity to make observations of the variance in radular length among the three forms. The three specimens were also of the same sex. The Newfoundland form held the smallest radula, as compared to mantle length, with *I. i. coindetii* from the Mediterranean having the largest. The South American form, *I. i. argentinus* had a radula intermediate in comparative size between the two.

Mangold, Lu and Aldrich (1969) speak of the Argentinian form being intermediate between the other two subspecies with respect to other characteristics, with particular reference to features incorporating cephalic structures and the brachial apparatus. It may be that this is a correct interpretation of *I. i. argentinus*, since the radular morphometry further supports this. Unfortunately, not only was a small (three) sample available to me, but very little detailed information on this form exists at present in the literature.

In the case of *I. i. illecebrosus*, it can be seen that the length and width of the radular ribbon increases as the mantle length increases, at a rate less than that of *I. i. coindetii* (Figure 1a and b, Figure 2a and b). Although the sample sizes were not sufficient to warrant extensive statistical analyses, it is suggested by the data that the growth in length of the radular ribbon of *I. i. coindetii* shows a greater rate of increase than that characterized in *I. i. illecebrosus*. It may be possible, therefore, to use radular length as one more characteristic on which to base subspecies identification, over the size range indicated.

By the use of computed indices (Figures 3 and 4) it is possible to attain almost complete separation of these two subspecies on the basis of radular morphometry. A more detailed study involving not only larger and more extensive samples, but also employing measurements of all tooth types, would, in my opinion, aid considerably in amassing information and criteria whereby the true relationship between these taxa might be established.

Not all Twentieth Century workers have accepted the subspecies concept as applied to the genus *Illex*. I contend that morphological and morphometric studies of the radular apparatus should be further exploited as a possible means in revealing the true relationships within this group.

I believe it is a safe assumption that a species may evolve without the occurrence of great structural modification. If *I. i. illecebrosus*, *I. i. coindetii* and *I. i. argentinus* prove in the future to be three separate species, it does not seriously affect the interpretation here presented of the basic similarity or near identity of the radular ribbons of these three forms. This situation may reflect nothing more than the fact that the genus is only recently evolved or is even now in a stage of evolution not yet affecting radular configuration.

Such infrasubspecific variations as seen in Plate 58 (Figures 1, 2 and 3) for *I. i. illecebrosus* may be due to a number of factors, including genetic variation, age or growth. The three specimens represented in this plate are from a restricted size range and geographic area and it is inferred that they are of the same age group. Perhaps of greatest significance is the situation seen in Figure 1, where a tricuspid condition of the lateral teeth is found. It is through plotting such individual variations in the radular teeth that we may be afforded the opportunity to observe the evolutionary processes, which I have just discussed.

Mangold, Lu and Aldrich (1969) have established that morphometric sexual dimorphism is characteristic of *I. i. coindetii* and lacking in *I. i. illecebrosus*. Again, referring to Figure 1b and Figure 2a, it becomes apparent that the male of *I. i. coindetii* exhibits a more rapid rate of growth in length of the radula than does the female of corresponding mantle length (Figure 2a and Figure 4c). This distinction between sexes is not evident in *I. i. illecebrosus* (Figure 1b and Figure 3c), which supports data presented by the aforementioned authors.

An examination of the sectionalized radular ribbon of *I. i. illecebrosus* (Plate 53) shows in Section A the region of tooth formation and development. In this region it can be seen that the newly formed teeth do not stain darkly, are narrow in width, and the curved or "wavy" tooth cusps indicate their soft or flexible condition. The teeth in rows A-6 to B-13 inclusive stain progressively lighter the greater their distance from the growing edge of the radular ribbon and the increase in their width is readily apparent. The teeth in rows B-14 to approximately C-25 are enclosed in the radular sac and are characterized by their high degree of cusp acuteness.

At this point it can be seen that the radular ribbon narrows and it is here, in this particular specimen, that the ribbon leaves the radular sac and curves over the muscular prominence which rises from the floor of the mouth. From this point to the anteriormost end of the radular ribbon the teeth are exposed in the buccal cavity and subject to use, accounting for their blunter cusps.

The ribbon narrows perceptibly from posterior (A) to anterior (D). The teeth are smaller in Section A, which supports the data of Nixon (1968) that as the animal increases in size the radular ribbon increases in length, width and the radular teeth are correspondingly larger. This same situation is seen in the radular ribbon of the larval *Rossia* sp. (Plates 12 a and b). The anteriormost portion of the radular ribbon is smaller, as are the teeth, since this area was formed first when the larva was smaller. It cannot be considered that these smaller teeth are a result of wear as this larva was taken from what remained of the egg membranes and therefore had not commenced feeding.

A Note on Phylogeny

There are many viewpoints concerning the interpretation of the cephalopod radula with regard to a particular type being either primitive or advanced. As stated earlier, Robson (1932) was of the belief that the homodont or unicuspidate condition characterized by *Argonauta* and the sepioids was the primitive condition for both the Octopoda and Teuthida. Brock (1880) may be cited as a representative of the opposite viewpoint, namely, that the heterodont condition seen in the genus *Ocythoe* and the ommastrephids was, in fact, a more primitive state of development. All of this conjecture was in the absnece of firsthand information on the configuration of the radula of extinct forms. It was not until 1967 that Lehmann published on the fossilized radula of an ammonite. For the first time, long-needed information was provided to cast its light upon this subject. The radular teeth of *Eleganticeras elegantulum* were found to be heterodont (Text Figure 1, page 21). This would indicate that early in the evolution of cephalopods the heterodont condition was well established tending to favour Brock. Certainly not enough information exists to settle this matter one way or the other. It must be realized, however, that a so-called primitive animal need not be considered primitive in all characteristics. Although a "homodont" dentition may be considered simple it need not be primitive and may represent a high degree of specialization in some of the teeth as is the case in the marginal teeth of *Nautilus pompilius* (Plate 7).

This whole area of discussion needs further information with respect to the function of the radula of the different species. It is possible that, given the necessary information, to use the morphology of the radular apparatus as an aid in taxonomy even to the species level.

G. C. Robson (1932) stated that "the morphology of the cephalopod radula is a difficult question". In addition, it is an important and most interesting one.

CONCLUSIONS

1. The configuration of the radular apparatus has been considered to be of taxonomic importance in all classes of molluscs.

2. While the general morphology of the radular apparatus among Coleoids is essentially similar, the variations in radular teeth between taxonomic groups, even to species level, are to a degree sufficient to be useful as a taxonomic character.

3. Since this has been found to be true, a valid and detailed description of the radula of any species is a desired and necessary part of the description of the species.

4. The function of the radular apparatus of Coleoids is to aid in the swallowing of food, while in Octopods the function is a more direct and active one, namely, in shell boring in feeding.

5. Both the radular ribbon and the radular teeth grow continually at the posterior end of the ribbon. In this way the radula not only grows in size but also teeth lost or worn through usage are replaced.

6. The radular ribbon and radular teeth increase in size as the individual animal increases in mantle length.

7. Only radular teeth located on that portion of the radular ribbon within the radular sac should be used as a taxonomic character.

Rows 15 through 20 are particularly desirable as they are well developed and unused. The anteriormost teeth on the radular ribbon are blunted and broken through use and therefore these are of little taxonomic value.

8. Newfoundland architeuthid radular teeth herein illustrated exhibit general similarities, however, individual differences among the five specimens examined outweigh the basic similarities. Doubt is cast on the earlier assumption that the five specimens are; all of one morphologically similar species. However, current and earlier Newfoundland specimens (1870's and 1930's) have similar radular teeth and demonstrate little similarity to those of eastern Atlantic origin.

9. The three subspecies of the ommastrephid *Illex illecebrosus* have a radular configuration similar in all three and it is not possible to separate them on the basis of radular morphology or tooth configuration. It is possible, however, to separate these forms on the basis of morphometric analyses of the radulae.

10. Apparently, radulae are sexually dimorphic in *Illex i. coindetii*, which is not the case with respect to the Newfoundland form.

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