SYSTEMATICS OF THE CEPHALOPOD FAMILY GONATIDAE FROM THE SOUTHEASTERN BERING SEA

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SYSTEMATICS OF THE CEPHALOPOD FAMILY GONATIDAE FROM THE SOUTHEASTERN BERING SEA

A

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ABSTRACT

The systematic relationships within the cephalopod family Gonatidae were examined utilizing specimens collected from the southeastern Bering Sea. Ten species; *Gonatus onyx*, *Gonatus madokai*, *Gonatus tinro*, *Gonatus berryi*, *Gonatus pyros*, *Gonatus* sp., *Gonatus* type A, *Berryteuthis magister*, *Berryteuthis anonychus*, and *Gonatopsis borealis*; were identified. Included in these are the identification of a probable new species, *Gonatus* sp., the verification of a questionable species, *Gonatus tinro*, and the classification of previously described but unclassified developmental stages. Morphometric characters were used for a retrogression analysis of each species' development.

The developmental stages for those species found in the study area are described and illustrated in detail. The taxonomic and morphometric characters of the species are compared. Two closely allied species, *Gonatus berryi* and *Gonatus* sp. are compared and contrasted. A brief analysis of the growth and development of the genus *Gonatus* is also given.

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CHAPTER 1

INTRODUCTION

Present Status of Cephalopod Research in the North Pacific Ocean

An understanding of the structure and functioning of biological communities can only be obtained if investigations include all aspects of those communities. Without this, it is impossible to make an accurate assessment of the trophic and spatial structure of the communities or the transformation of matter and energy. The present knowledge of subarctic pelagic communities almost completely excludes one of the most abundant and ecologically important members — cephalopods. The majority of available information on pelagic cephalopods from the North Pacific has been the secondary product of biological and ecological research on other organisms. Salmonid fisheries investigations (Allen and Aron, 1958; Favorite, 1970; Ito, 1964; Kanno and Hamai, 1971; LeBrassuer, 1966; Manzer, 1968; and Nishiyama, 1974), sea bird studies (Ogi, 1980; Ogi and Tsujita, 1973; and Wehle, 1976) and marine mammal research (Akimushkin, 1955; Clemens and Wilby, 1933; Clements *et al.*, 1936; Fiscus and Baines, 1966; Fiscus *et al.*, 1964; Kenyon, 1956; North Pacific Fur Seal Commission Reports, 1962, 1969, 1971 and 1975; Okutani and Nemoto, 1964; Okutani and Satake, 1978; Okutani *et al.*, 1976a; Wilke and Kenyon, 1957; and Wooding, 1955) indicate that the North Pacific and Bering Sea support a large pelagic cephalopod fauna. The few studies which have dealt exclusively with the cephalopods of this region (Akimushkin, 1963; Berry, 1912, 1913 and 1925; Clarke, 1966;

Filippova, 1971; Kodolov, 1970; Laevastu and Fiscus, 1978; Nesis, 1973a; Okutani and McGowan, 1969; Pearcy, 1965; and Sasaki, 1920 and 1929) are either limited in scope or handicapped by the deficient state of cephalopod systematics. Notable exceptions to this are Young's (1972) systematic study of the pelagic cephalopods of California and Kubodera's (1978) morphological comparison of the family Gonatidae.

The inability of conventional methods to adequately sample adult populations is probably the major reason for the shortcomings in cephalopod research. This problem was circumvented by Okutani and McGowan (1969) when they found that large numbers of pelagic cephalopod larvae could be collected with conventional plankton and micronekton nets. They further indicated that these collections offer an excellent opportunity to delineate the species composition of an area, as well as provide an indication of the times and places of spawning, the developmental history, and, possibly, the abundance of many species. The applicability of this approach, however, has been restricted by the limited knowledge of larval cephalopod systematics.

Many of the larval stages of species which occur in the western North Pacific, the Bering Sea, and waters surrounding Japan have already been documented (Kubodera, 1978; Kubodera and Okutani, 1977; Okiyama, 1965; Okutani, 1966, 1968, 1969, 1974, 1975 and 1978; Okutani *et al.*, 1975 and 1976b; and Yamamoto and Okutani, 1975). Similar work has also been done for areas off California (Okutani and McGowan, 1969). Few of these larvae, however, have been identified to the species level and many were incorrectly identified. Voss (1977) indicates that this

problem is commonplace because the developing cephalopod larvae exhibit various characteristics, both morphological and physiological, which may be impossible to relate to the adult forms.

Kubodera (1978) was the first to attempt to delineate the developmental history of a single family. His work, the completeness of which was limited by the availability of adult specimens, has provided an excellent basis for further studies.

The present work attempts to clarify many of the existing systematic problems within the family Gonatidae. Several previously described, but undetermined, larval types have been classified, including the early developmental stages of *Gonatus onyx*, *Gonatus tinro*, and *Gonatus* sp., by tracing the developmental morphology of each species found in the study area. Additionally, a probable new species of *Gonatus* has been described along with a verification of the authenticity of *Gonatus tinro*. The validity of this species has been questioned due to a lack of specimens. In several cases the descriptions given herein paraphrase descriptions of previously documented species; however, it was felt that full descriptions were critical for tracing the taxonomic characteristics of each species.

Early Life History: A Synopsis

It is generally agreed that cephalopod development is direct, without the formation of a true larval stage; with the term larval being commonly applied to those developmental stages between hatching and maturity (von Boletzky, 1974 and 1977; and Voss, 1977). Nesis (1979,

p. 267) in his review of this concept felt that "development may be viewed as direct only when all the material of the rudiments of the embryo body are completely transformed into the corresponding parts of the adult body of the animal; if, in the course of development, temporary organs appear, such a development cannot be regarded as direct." He further argues that "all cephalopods, without exception, have transitory organs connected with swallowing and assimilating a large mass of yolk" and concludes that "there is no direct development in any of the cephalopods." von Boletzky (1974, p. 57) on the other hand postulates that "the so-called 'larval' features, such as lack of arms and fusion of tentacles, should not be so much stressed as 'transitory' formations, but rather as functional adaptation of 'adult equipment' to a young animal of extremely small size." Both authors agree, however, that postembryonic development of cephalopods requires a special definition which is valid for all members.

The following synopsis of the early life history of cephalopods is based largely on the works of von Boletzky (1974 and 1977) and Nesis (1979). In all cephalopods the length of embryonic development is related to egg size, which is relatively constant within a species, and to environmental temperature. Within the range of temperature adaptation of a species the length of embryonic development decreases with higher temperature (McMahon and Summers, 1971 and Summers, 1968 and 1971). At a given temperature, the relation between egg size and length of development varies greatly between species but large eggs generally tend to have a longer developmental time than small eggs.

Generally speaking, the small eggs of pelagic cephalopods produce planktonic young which are usually morphologically different from the adult. Large eggs, however, generally produce much more adult-like animals in both appearance and behavior. Considering the cephalopod orders separately, all Sepiodea have relatively large eggs with the newly-hatched young having a life style similar to the adult. The pelagic species of this order (members of the genera *Spirula* and *Heteroteuthis*) are planktonic. The other members of this order are all benthic and produce benthic young. The only known exception to this is *Idiosepius pygmaeus*, the "pygmy Cuttlefish." This benthic species has very large eggs that produce planktonic young (Natsukari, 1970).

The Teuthoidea are all nektonic, some (members of the suborder Myopsida) live in nearshore waters and often close to the bottom, the majority (members of the suborder Oegopsida) are pelagic. The newly-hatched young of both suborders are planktonic, even though members of the Myopsida produce relatively large eggs.

Specializations such as the fusion of tentacles, lack of or extremely small size of certain arms, and other morphological variations are evident on many planktonic stage cephalopods. Generally speaking, the planktonic young of a species are equipped with relatively shorter arms and longer tentacles than the adult stage. It is important to note, however, that although reduced in size, these structures are equipped with functional suckers that have exactly the same prehensile abilities as the adult. This specialization suggests that even the smallest of these planktonic animals are active predators.

Adaptations for swimming and stabilization are extremely important in the planktonic stage of development. Stabilization and sinking are controlled either by fin and/or funnel activity, or passively by adjusting the animal's density. The latter is accomplished by the use of chambered shells containing gas or by the secretion of body fluids which are less dense than sea water (Clarke *et al.*, 1969 and 1979; and Denton and Gilpin-Brown, 1961 and 1973).

Planktonic cephalopods have been reported capable of maintaining a considerable swimming speed (Zuev and Nesis, 1971). Packard (1969) analyzed the movement of newly-hatched, juvenile and adult *Loligo vulgaris*. For newly-hatched animals he measured a maximum velocity of 16 cm/sec and for juveniles 128 cm/sec. He also observed that mantle contractions were repeated many times for swimming at high speed. These data indicate that the planktonic young of cephalopods are extremely mobile and could conceivably cover considerable distances.

Benthic young differ in their manner of locomotion although the basic mechanism is the same. In *Sepia* neutral buoyancy is achieved by the cuttlebone; the use of the fins, which form an undulating margin, allows these animals move and maneuver with a minimum of funnel activity. Sepiolids, however, show an intense fin and funnel activity when hovering in mid-water (Denton and Gilpin-Brown, 1961). Young Sepiolids, particularly *Rossia*, may also exhibit a crawling movement similar to benthic octopods (von Boletzky and von Boletzky, 1973).

Some species of benthic young have unique morphological adaptations. The integumental muscles of the ventral surface of the mantle and the

flattened ventral surface of the arms act as large suckers which enables the young of *Sepia officinalis* to attach itself to a hard substrate (Naef, 1923). Young animals can thus withstand water current of considerable strength.

Survival depends to a large extent on the ability to elude potential predators by concealment or escape. The equipment and related behavior that are found in the adult are also found in young cephalopods. A functional ink sac is available in all known decapods except for the subfamily Rossiinae. Young cephalopods also possess to a greater or lesser degree functional irridophores, photophores, and chromatophores. These features enable the young animals to show various concealment and countershading patterns and, in the case of benthic young, to mimic the background.

The ecological role of cephalopods in the pelagic ecosystem has not been evaluated. This is epecially true of the importance of these animals as predators and competitors and consequently as vectors for the transfer of matter and energy. Lipinski (1973) and Zuev and Nesis (1971) have given theoretical overviews of this aspect; however, only a few works have examined the food habits of adult cephalopods: Fields (1965) for *Loligo opalescens*, Naito *et al.* (1977) for four oceanic species, Okiyama (1965) for *Todarodes pacificus* and Vovk (1972) for *Loligo pealei*. The feeding habits of juvenile *Gonatus fabricii* were reported briefly by Nesis (1964).

Hurley (1976) has been the only researcher who has closely documented the feeding habits of young squid. It was observed that the

amount of food consumed by young *Loligo opalescens* averaged about 50% of the predator's body weight per day. Further it was estimated that, "at this rate, a newly hatched squid would consume 150 nauplii (*Artemia*) or 14 anchovy larvae per day, while a 7 mm squid would consume 1,500 nauplii or 135 anchovy larvae per day" (Hurley 1976, p. 181). This information, combined with densities of young squid up to 8312 per 1000 m^3 in the Bering Sea (unpublished data), indicates that juvenile squid could have a tremendous impact on prey populations especially if they concentrate on a specific food type.

Historical Review

The first member of the family Gonatidae was described (in part) by Fabricius in 1780 under the name *Sepia loligo* (Berry, 1912; Middendorff, 1849; Naef, 1923 and Steenstrup, 1880). This species was classified *Onychoteuthis fabricii* by Lichtenstein (1818) and endured several other synonyms until Hoyle (1886) established the family Gonatidae. Prior to Hoyle's (1886) work, a second member of this family, *Onychoteuthis kamtschatica*, was described by Middendorff (1849) from the North Pacific. Gray (1849) also established the genus *Gonatus* during the same year but again the generic name did not come into common use until after 1886. Lönnberg (1898) added a third species, *Gonatus antarcticus*, from the Antarctic.

Berry (1912) described what he considered a young stage of *Gonatus fabricii* but later revised this and included it in the family as a new species, *Gonatus magister* (Berry, 1913). Naef (1921) noted that

Berry's (1912) description of the club of this form differed so drastically from other members of the genus *Gonatus* that he established it as the type specimen for a new genus, *Berryteuthis*. He justified the establishment of this genus by pointing out that "*Berryteuthis* has fins of the type of the Entoploteuthidae which occupy more than half of the mantle length. It has no hooks on the club, and the suckers on the club show a different more normal arrangement; there are more than eight longitudinal rows which do not merge to form a bare median area on the hand part and reach proximally to the distal third of the stalk, also without leaving a bare stripe between them" (Naef, 1923, p. 227). Regardless of his analysis the validity of this genus was questioned until Roper *et al.* (1969, p. 6) authenticated it; they state, "this genus has previously been considered a synonym of *Gonatus* or at best a subgenus. However, with the recent discovery of a number of new species of *Gonatus*, the generic differences are more clearly defined and the evidence indicates that *Berryteuthis* should be considered a valid genus."

Sasaki added a third genera and two additional species to the family with his description of *Gonatopsis octopedatus* (Sasaki, 1920) and *Gonatopsis borealis* (Sasaki, 1923). During this same period Naef (1923) reevaluated a description of *Gonatus fabricii* given by Berry (1912) and from this he proposed the addition of a new species, *Gonatus berryi*, to the genus *Gonatus*. Again, the validity of this species was not clearly established until Young (1972) authenticated Naef's (1923) evaluation of Berry's (1912) specimen.

From 1923 to 1963 the literature is void of systematic works on the Gonatidae. The first of many new species was added when Pearcy and Voss (1963) described *Gonatus anonychus* from off the Oregon coast. This species has since been relegated to the genus *Berryteuthis*. Okutani and Nemoto (1964) described a subspecies of *Gonatopsis borealis*, *Gonatopsis borealis makko*, from the stomach contents of sperm whales taken in the Bering Sea. Young (1972) elevated this to the species level. He states, "this form differs from *G. borealis* primarily in having a slenderer mantle, longer arms (two-thirds of the M.L. versus two-fifths of the M.L), a slightly different arm formula, and smaller fins. These differences are sufficient to indicate that *G. b. borealis* and *G. b. makko* should be considered as distinct species and not as subspecies" (Young, 1972, p. 61). Okiyama (1969) included a fourth species in the genus *Gonatopsis* with his description of *Gonatopsis japonicus* from the Japan Sea.

Three new species, *Gonatus onyx*, *Gonatus pyros* and *Gonatus californiensis*, were added by Young (1972) and two additional species and a subgenus, *Gonatus (Egonatus) tinro* and *Gonatopsis okutanii* by Nesis (1972). The most recent addition to this family, *Gonatus madokai*, was made by Kubodera and Okutani (1977). Imber (1978) also advanced a new species, *Gonatus phoebetriae*, from the antarctic ocean; however, his addition was based on a single lower beak found in the stomach of a sooty albatross and as such will require additional specimens to validate the species.

CHAPTER 2

MATERIALS AND METHODS

Study Area and Sampling Methods

The cephalopod larvae described in this report came from zooplankton collections made in the eastern and central Bering Sea during the T/V *Oshoro Maru* cruises OS065, June, 1977; OS070, June, 1978; and OS075, July, 1979. The samples were preserved aboard ship in 7% neutral formalin and seawater solution and transferred to a 40% isopropyl alcohol solution at the laboratory. During these cruises surface and subsurface collections were made in water depths ranging from 35 to 4000 m.

Surface collections were made using a 1.3 m diameter x 4.5 m ring net with a mesh size of 2 mm in the forward 3 m and 0.333 mm in the cod end. The duration of the ring net tows was 10 minutes at a speed of 2 knots. Subsurface collections were made in 1977 and 1978 using a series of five 0.56 m diameter x 2 m MTD closing nets, mesh size 0.35 mm throughout, which were fished concurrently at depths of 5, 10, 20, 35 and 50 m. The duration of the MTD net tows was 15 minutes at a speed of 1.5 knots.

A 2 m^2 tucker trawl, 2 mm mesh size throughout, was also employed during these cruises. The duration of these tows varied from 30 minutes to one hour at a speed of two knots. The net was fished at various depths (between 0 and 1000 m) which corresponded with a good return echo on the ship's depth finder. The exact depth to which the net was fished was determined by the use of chemical sounding tubes.

The volume of water filtered by the MTD nets was measured by flow meters suspended in the mouth openings. The volume of water filtered by the ring net and the tucker trawl was calculated from an assumed filtering efficiency of 100%, the effective mouth opening, speed of the ship, and duration of tow. The density of the squid larvae was then calculated in numbers/1000 m^3.

The station positions and numbers are illustrated in Figures 1-3. Samples from a total of 27 out of 42 stations occupied during 1977, 21 out of 55 stations from 1978, and 28 out of 40 stations from 1979 contained squid larvae. The species composition, densities of cephalopod larvae, number of stations at which each species was taken, and range of number of individuals taken for each year are given in Appendix A.

No attempt was made to examine the efficiency of the sampling method; however, the method employed is analogous to that utilized by Okutani and McGowan (1969). Their study compared the efficiency of six plankton nets ranging in diameter from 20 to 140 cm with a mesh size of 0.65 mm. They concluded that the nets used were "inadequate for measuring absolute abundance of larval squid or for indicating their actual presence at low population densities" (Okutani and McGowan, 1969, p. 5). Ida (1972) also noted that the collecting efficiency of simultaneously towed, various sized, ring nets of 0.5 and 1.0 mm mesh size varied considerably in both number and size of organisms taken. Considering these facts the effectiveness of the sampling method employed for determining the cephalopod fauna of the study area is questionable. This is especially true for low density species.

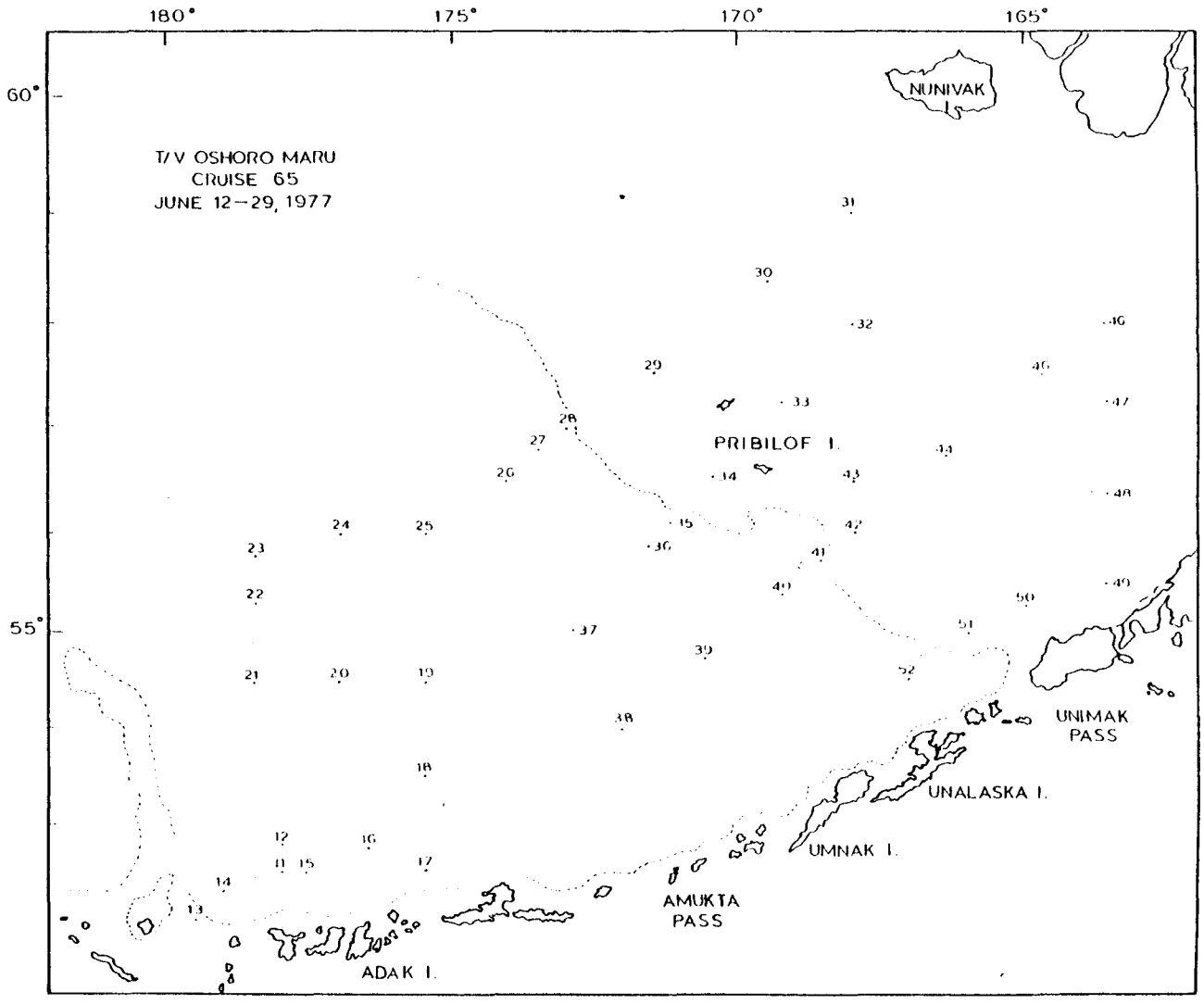


Figure 1. Sampling station locations, 1977.

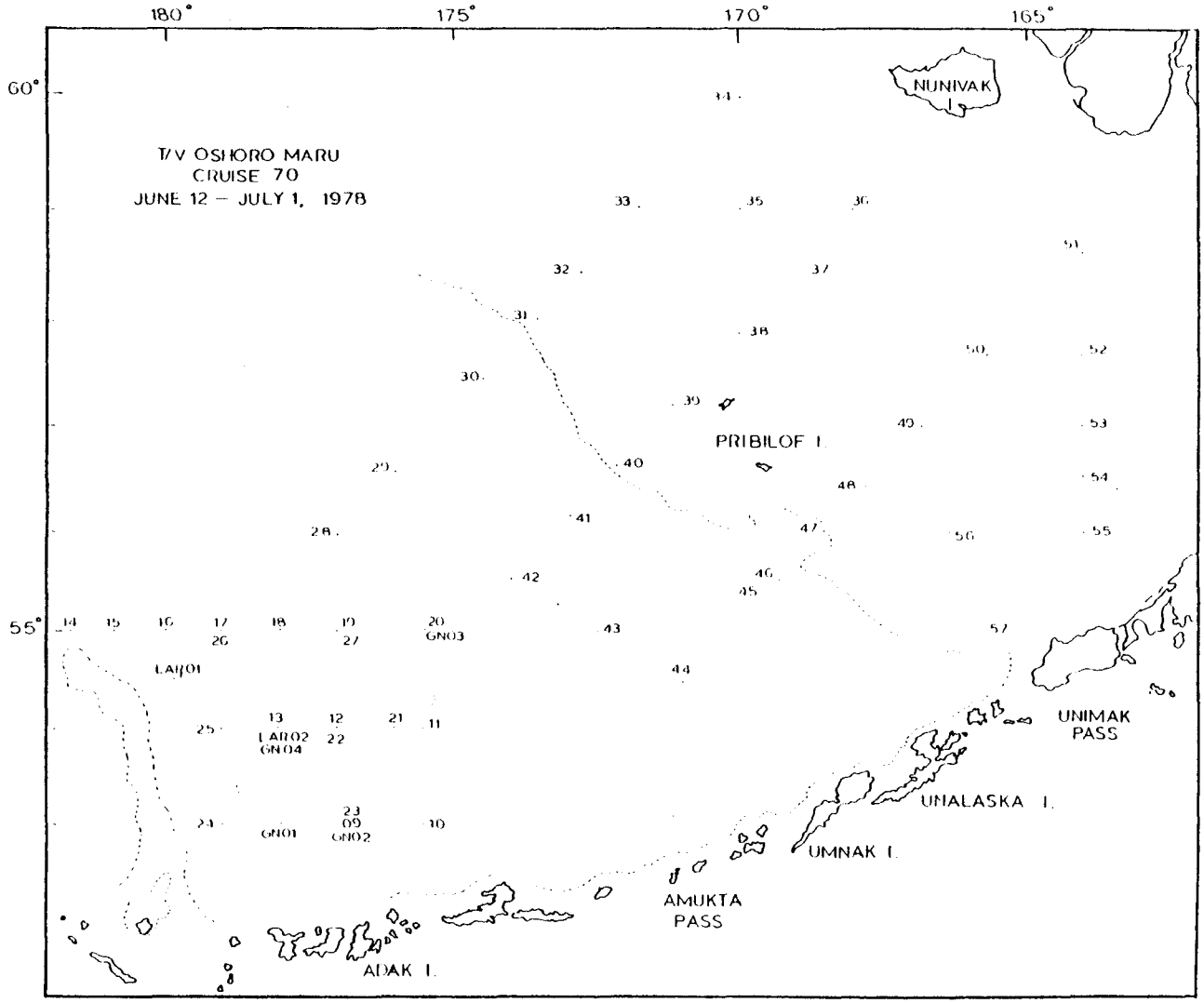


Figure 2. Sampling station locations, 1978.

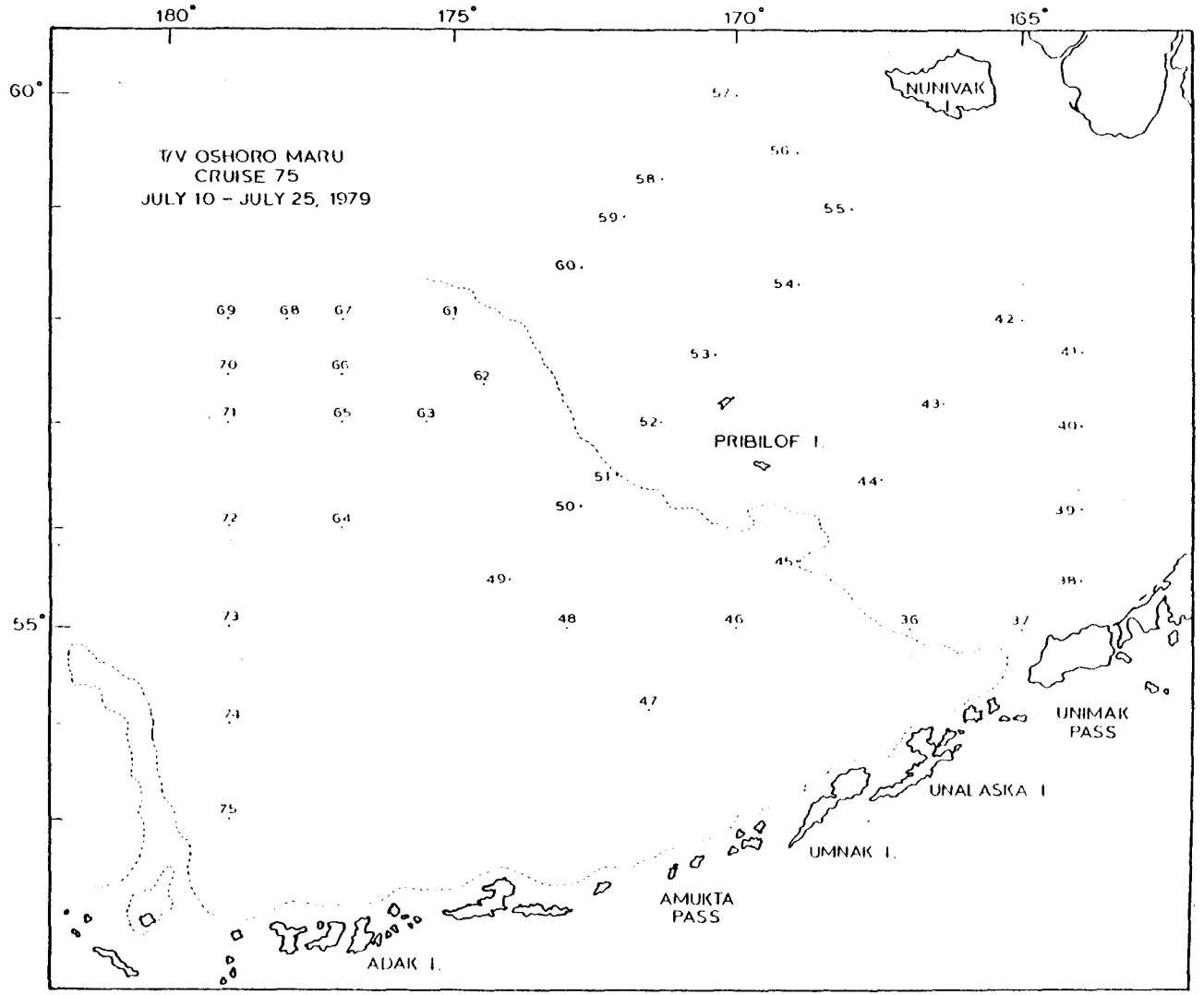


Figure 3. Sampling station locations, 1979.

Description of Measurements

Most of the morphological measurements utilized in the systematic aspect of this study are those which are commonly employed in the literature (Cohen, 1976; Haefner, 1964; Lu, 1963; Roper *et al.*, 1969; Voss, 1956; and Wormuth, 1976) and are graphically represented in Figure 4. Measurements were taken to the nearest 0.01 mm utilizing either a measuring ocular, calibrated to 0.01 mm, mounted in an Olympus binocular dissecting microscope or by the use of an Olympus measuring microscope, calibrated to 0.001 mm. The abbreviations and definitions of the measurements and indices used in this study are as follows:

DML, dorsal mantle length: measured from the posterior most point to the anterior most point of the dorsal side of the mantle.

MW, mantle width: extended width of the mantle at the mantle opening.

FL, fin length: measured from the posterior tip of the united fins to the farthest point on the anterior border of the fin.

FW, fin width: greatest width across both fins.

PL, pen length: distance from the posterior tip to the anterior tip of the pen.

I, II, III, and IV; length of the dorsal (I), dorso-lateral (II), ventro-lateral (III), and ventral arms (IV): measured from the distal tip to the dorsal point of attachment on arms II and III and to the junction between arms I and IV.

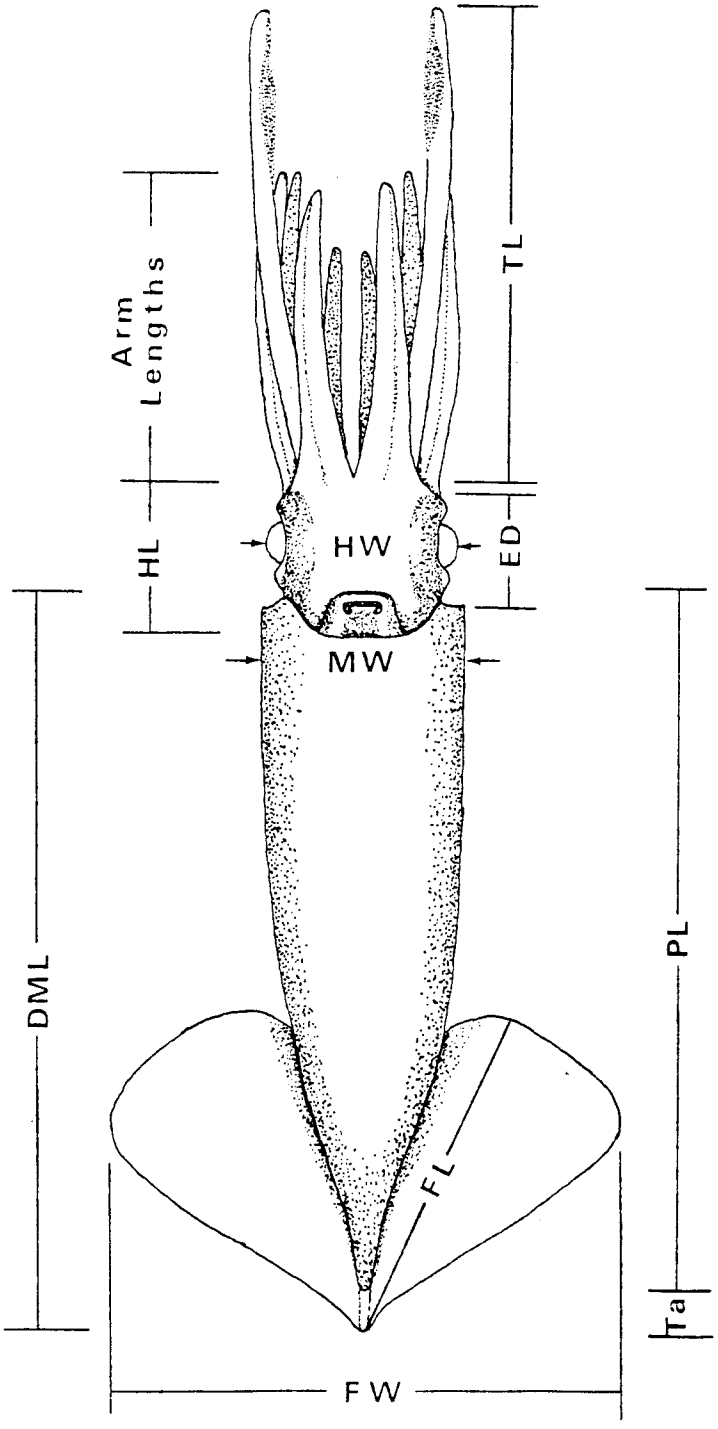


Figure 4. Morphological measurements (see text for explanation of abbreviations).

HL, head length: measured from the anterior edge of the nuchal cartilage to the V-shaped juncture of arms I.

HW, head width: distance across eyes.

T, tentacle length: measured from the dorsal point of attachment to the distal tip.

CL, club length: measured from the distal end of the tentacular stalk to the distal tip of the dactylus.

ED, eye diameter: greatest diameter of eye.

All indices utilized and listed below are the indicated measurement expressed as a decimal fraction of the dorsal mantle length.

MWI: mantle width index.

FLI: fin length index.

FWI: fin width index.

HLI: head length index.

HWI: head width index.

TI: tentacle index.

EDI: eye diameter index.

The conventional method of determining the MW is by measuring either the greatest distance across the mantle or the greatest distance across the mantle opening with the mantle held as cylindrical as possible. Due to the size and flacidity of the larval mantle, and consequently the difficulty experienced in trying to maintain a cylindrical shape, it was felt that the use of an extended mantle width would provide a more

accurate measurement. In obtaining this measurement the mantle was gently expanded to its widest extent by the insertion of a pair of fine larval tweezers into the mantle opening. The measurement was then taken across the extended mantle opening. Pen lengths were obtained *in vivo* due to the difficulty in removing the entire gladius intact.

For comparison all measurements were converted to a relative size as a decimal fraction of the DML. The mean and standard deviation of the relative size of each character was then computed (Appendix B). Frequency distributions were employed to further evaluate developmental changes. The relationships between the development of the arm and club armature and the pen length was compared to determine the sequence and timing of developmental changes and the systematic importance of these changes.

No attempt was made to quantitatively analyze the chromatophore patterns. The chromatophore number and arrangements were determined as an 'average' of several observations. In many instances the majority of the mantle's epidermis, and consequently the chromatophores, was missing. In these cases an evaluation was made from the remaining epidermis. The chromatophores on the head, tentacles, and arms usually remained intact and consequently a more precise evaluation of these was accomplished.

Scanning electron microscophy (SEM) was used to determine the structure of several larval radulae. Several authors (Aldrich *et al.*, 1971; Hickman, 1977; Kristensen, 1977; Radwin, 1969; Risso-Dominguez, 1961; Solem, 1972; Solem and Roper, 1975; and Turner, 1960) have demonstrated

the techniques and applicability of this method for studying minute cephalopod structures.

The buccal mass, containing the beak and radula, was removed intact from the cephalic region. This was accomplished by applying gentle pressure on the dorsal and ventral surfaces of the head slightly posterior to the points of attachment of arms I and IV. The buccal mass was then soaked for 24 to 48 hrs. in 10% room temperature NaOH until the tissue was easily removable (Lindberg, 1977). After removal from the NaOH solution the tissue was gently teased away from the radula by the use of minuten dissecting needles.

The extracted radula was transferred to a small vial containing a 70% solution of ethyl alcohol. The vial was then partially emersed in an ultrasonic cleaner for 5 seconds. This served to remove any film left by the NaOH, any remaining tissue, and to dilute any colloidal suspensions. The radula was then soaked in a clean solution of 70% ethyl alcohol for 24 hours.

After soaking the radula was mounted on an SEM stub with rubber cement; Solem (1972) found that this mounting medium produced a firm bond and did not allow the radula to sink into or become covered by the compound. A small amount of rubber cement was placed on the SEM stub and covered with several drops of the same alcohol concentration in which the radula had been soaking. This prevented the cement from drying until the specimen was in position. After the specimen was placed on the cement and manipulated into the desired viewing position it was

coated with 200 angstroms of gold in an SPI stutter coater and viewed on a JSM 35U scanning electron microscope.

Systematic Characteristics of the Family Gonatidae

The family Gonatidae is divided into three genera: *Gonatus*, *Berryteuthis*, and *Gonatopsis*. All members of this family are characterized by tetraserial armature on the arms, a simple straight funnel locking cartilage, and buccal connectives of the DDVV type, Figure 5 (Roper *et al.*, 1969; and Young, 1972). A single exception to these characteristics is found in *Gonatopsis octopedatus* where the arm tips are covered with numerous rows of minute suckers (Sasaki, 1920).

The genus *Berryteuthis* is characterized by a radula with seven longitudinal rows of teeth and the absence of hooks on the tentacular club (Nesis, 1973b; and Roper *et al.*, 1969). Young (1972) characterized the genus *Gonatus* as having a complex tentacular club which carries at least a single large central hook and only five longitudinal rows of radular teeth. *Gonatus tinro* (Nesis, 1972), which has only suckers on its tentacular club, is an exception to these characteristics and prompted Nesis (1973b) to propose a revised hierarchy. He suggested that the genus *Gonatus* be subdivided into two subgenera *Gonatus* and *Eogonatus*; the subgenus *Gonatus* to accommodate those species with hooks on the tentacle and the subgenus *Eogonatus* to accommodate *Gonatus tinro*.

Members of the genus *Gonatopsis* are characterized by the atrophy of the tentacles in all but the larval stages (Roper *et al.*, 1969; and Young, 1972). Nesis (1973b) also proposed that this genus be subdivided

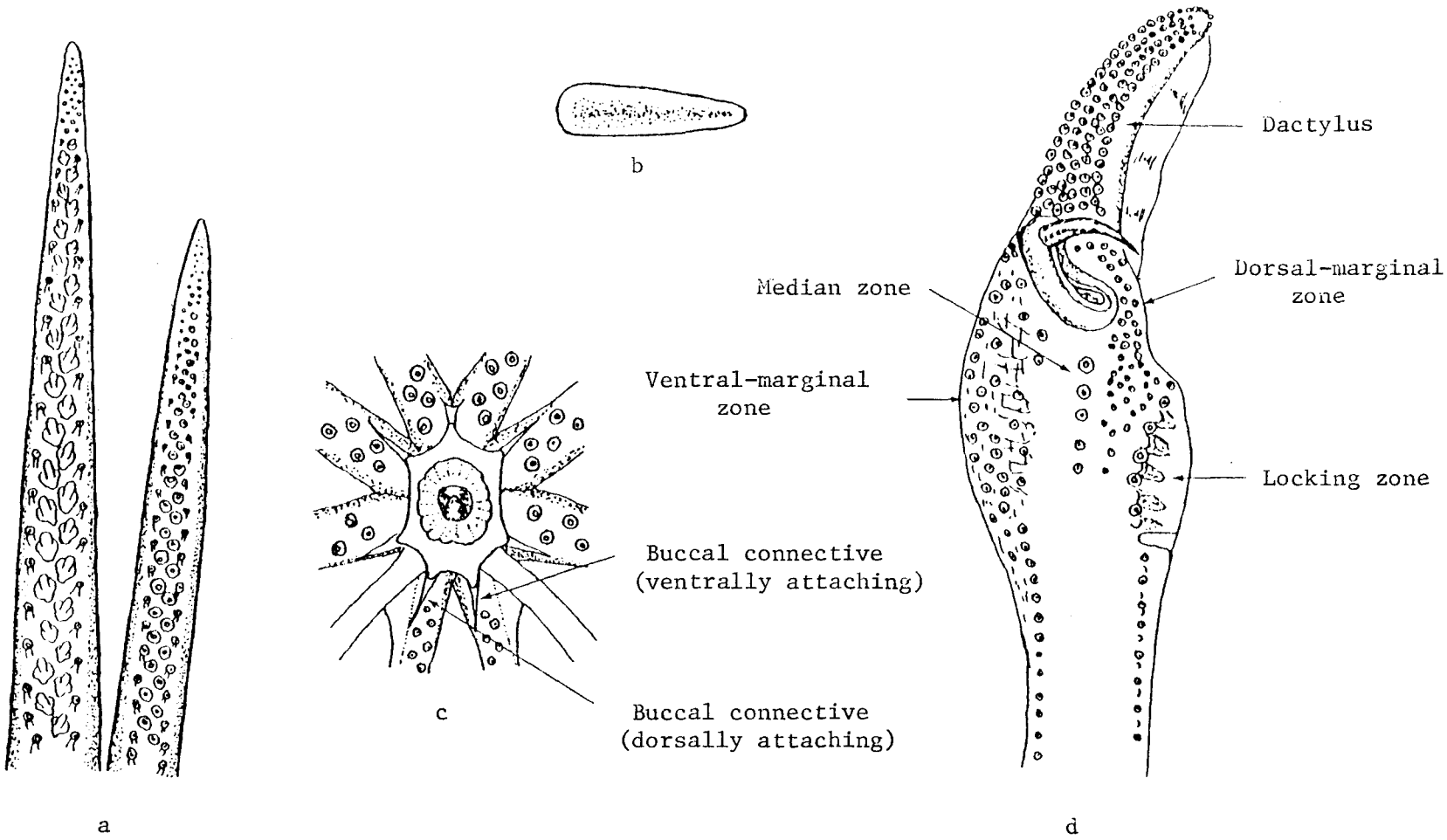


Figure 5. Systematic characteristics of the family Gonatidae: (a) tetraserial armature of arms III and IV, (b) simple, straight funnel locking cartilage, (c) oral surface of brachial crown showing buccal connectives, and (d) oral surface of tentacle showing major features (b and c redrawn from Roper *et al.*, 1969).

into two subgenera, *Gonatopsis* and *Boreoteuthis*. Members of the subgenus *Gonatopsis* having a radula with five longitudinal rows of teeth, whereas the radula from members of the subgenus *Boreoteuthis* consists of seven longitudinal rows of teeth.

Kubodera and Okutani (1977) felt that Nesis' (1973b) revision was premature due to the probable existence of more sympatric species of *Gonatus* from the northern Pacific Ocean. Young (1972) has also pointed out that *Gonatus fabricii* from the Atlantic Ocean has not been adequately characterized and that additional species from this family probably exist in the Antarctic areas as well as the North Pacific. From the information available at this time Nesis' (1973b) proposed hierarchy for the family is reasonable, especially since the present study includes a large number of *Gonatus tinro*; however, without an adequate characterization of the family from all areas, revisions will undoubtedly take place.

Differentiation of Cephalopod Development

Regardless as to whether cephalopods possess a true larval stage or whether development is direct, the division of cephalopod development into growth stages is an extremely helpful descriptive tool. Kubodera (1978) has outlined a system for the separation of young Gonatid squids into developmental stages. The characteristics which were selected as determinants of development were based on two critera: (1) the development of the characteristics is common in all species and (2) the characteristics are both systematic and ecological indicators.

He selected the development of the tentacular armature as the developmental indicator for those species which possess a tentacle and for those species which lack tentacles the development of the arm armature.

To conform with the use of external characteristics as indicators of change the immature and adult stages defined by Kubodera (1978) have been combined into an adult stage with sexually mature and sexually immature components. For additional convenience in describing the development of each species the developmental stages have been further separated into early and late phases. The early phase is defined as that point in development when the characteristics of each stage are just beginning to appear. Conversely, the late phase is that point when the characteristics of each stage are fully evolved. It should be kept in mind that the use of developmental stages is a convenience tool only; consequently, a wide variety of gradients in each developmental stage will be observed. The breakdown of developmental stages used for Gonatid squid in this report is as follows:

Adult stage: armature of the tentacles and arms are fully mature (i.e., suchers and hooks are fully developed).

Adolescent stage: armature of the tentacular clubs are similar to the adult stage but hooks are not differentiated or immature hooks are present; alternately, the median rows of arms I-III are metamorphosing from suckers into hooks.

Post-larval stage: armature of the tentacular club is made up exclusively of sucker and hook buds; alternately, the median rows of arms I-III are suckers.

Larval stage: tentacular clubs are not developed but are evident as a clear area at the distal tip of the tentacles; alternately, the arm armature is changing from sucker buds into suckers.

CHAPTER 3

SYSTEMATICS

Class Cephalopoda
Order Teuthoidea
Family Gonatidae Hoyle, 1886
Genus *Gonatus* Gray, 1849

Gonatus onyx Young, 1972

Adult Stage

The mantle (Plate 1) is relatively thin but muscular, and generally cylindrical in shape with a MWI = 0.27. The free anterior margin has two ventrolateral projections corresponding with the mantle portion of the funnel-mantle locking cartilage. Situated between these projections is a depression in the ventral margin which accommodates the funnel. Posteriorly the mantle tapers gradually to a conical terminus. A long gelatinous tail (TaI = 0.15) originates from the dorsal margin of this terminus.

The head is wider than long (HLI = 0.26 and HWI = 0.32) with large prominant eyes (EDI = 0.19) which occupy about 90% of the lateral portions of the head. There are three nuchal folds posterior to each eye. The nuchal cartilage (Plate 3d) is generally rectangular in shape with rounded anterior and posterior margins. There is a distinct median ridge with a narrow and deep central groove followed laterally by wide shallow grooves and indistinct marginal ridges.

The fins are large (FLI = 0.40 and FWI = 0.69), thin, and muscular. The posterior margin is concave with the proximal border attenuating along the tail. The anterior and lateral margins are convex and large

free anterior lobes are present. All body surfaces are covered with small densely packed chromatophores.

All arms are well developed and muscular with arms II and III slightly thicker and more muscular than I and IV. The arm formula is II>III>IV>I; with arms I = 38% of DML, II = 52% of DML, III = 51% of DML, and arms IV = 47% of DML. The arm armature is in the four staggered longitudinal series common to this family. The lateral two longitudinal rows consist of small suckers which are attached to the trabeculae of a well developed supporting membrane by short peduncles (Plate 3a). The dentition of the lateral series is from six teeth in the smaller distal suckers to eight teeth in the larger more proximal suckers. The median two longitudinal rows consist of large sheathed hooks (Plate 3b). The hooks increase in size from the proximal portion distally to the middle of the arm and then decrease in size toward the distal tip. The armature of arms IV consist of four longitudinal series of suckers. The two lateral rows are consistant with those of arms I-III but with a reduced supporting membrane. The median longitudinal rows consist of larger suckers attached by short peduncles. The dentition of these suckers is the same as the lateral suckers of arms I-III. Arms IV have well developed lateral swimming keels along their entire length.

The tentacles (Plate 2a) are relatively short, thick and strong (TI = 0.47). The club is moderately short (34% of TL) and complex in structure. The dactylus supports a distal circlet consisting of eight small smooth ringed suckers and four proximal longitudinal series of suckers. At the confluence of the dactylus and manus the four

longitudinal rows expand to six indistinct rows. The dentition of these suckers is 6-8 inner ring teeth (Plate 2b). A dorso-aboral keel is present on the dactylus.

The ventral-marginal zone supports four rows of suckers which decrease in size medially. The number of longitudinal rows decrease distally to one which terminates behind the large central hook. Proximally the armature of this region also decreases to one row which is continuous with a ventral row of suckers on the stalk. Suckers from this zone are supported by strong peduncles which are attached to trabeculae originating from the medial portion of the manus. Suckers of this region have 11-13 teeth (Plate 2c).

The dorsal-marginal zone has a maximum of six longitudinal rows of suckers which decrease both proximally and distally. Proximally the suckers terminate just beyond the last sucker of the median zone while distally the rows decrease to two which pass lateral to the large central hook and merge with the suckers of the dactylus. The dentition of suckers from this region is 5-7 teeth on the distal margin of the inner ring (Plate 2f).

The locking zone consists of five alternating ridges and grooves. Each ridge has one large smooth ringed sucker at its medial most edge (Plate 2e). These suckers alternate with large, spherical, fleshy knobs which are recessed at the medial most margin of each groove. Distally there is one smooth ringed sucker without a corresponding groove or ridge. Proximally the zone ends with a distinct break in

the musculature. This break is reinforced by a membrane which attaches distally to the locking zone and proximally to the stalk.

The median zone consists of five proximal suckers, each of which contain from 5-7 teeth (Plate 2d), and one large distal hook. The suckers decrease in size proximally with the largest being just proximal to the large central hook. In the specimen examined there was no evidence of a hook distal to the central hook nor was there evidence of an enlarged sucker which could modify into a hook. Young (1972, p. 44) states, "usually, there is no member of this zone distal to the large hook; however, occasionally an enlarged sucker lies behind the hook. Sometimes this sucker may bear an enlarged tooth on the distal margin of the inner ring; and, rarely, this is developed into a small, but completely formed hook."

The stalk carries two longitudinal series of suckers, one along each margin. The row along the ventral margin is continuous with those of the ventral marginal zone. Young (1972, p. 45) described the row along the dorsal margin as "consisting of alternating suckers and pads with adjacent ridges that show faint resemblance to the locking apparatus of the manus; traces of the fleshy ridges accompany only the first few suckers, then disappear."

The funnel organ (Plate 3e) consists of paired ventral oval pads and a single V-shaped dorsal pad. Posteriorly each arm of the dorsal pad widens abruptly to produce distinct shoulders and a triangular shaped terminus. Anterior to the shoulders each arm supports a median longitudinal ridge which extends to near the apex. At the apex and midway

between the longitudinal ridges a single slender papillae is attached. Two anterior lateral processes impart a distinct U shape to the anterior margin. Each funnel locking cartilage (Plate 3c) has a single straight groove which corresponds to a straight cartilaginous ridge on the mantle. The locking cartilage is lanciform, with the anterior margin narrower than the posterior margin.

Adolescent Stage

The mantle of the adolescent stage (Plates 4a and 5a) generally exhibits the same characteristics as the adult stage but is more swollen in appearance (MWI = 0.51-0.61). Additionally, the early adolescent phase has a slightly separated transparent epidermis with a distinct chromatophore pattern; a pair on the dorsal midline near the base of the fins, one on the dorsal midline near the posterior one-third of the mantle and four on each lateral midline. The late adolescent phase is sparsely covered with moderately large randomly placed chromatophores. As in the adult the free anterior ventral margin of this stage also has projections at the locking cartilages with a funnel depression between them. The posterior margin tapers more abruptly and presents a more rounded outline than the adult stage. A proportionally shorter gelatinous tail is present (TaI = 0.06-0.08).

The head width is greater than the head length (HLI = 0.19-0.27 and HWI = 0.27-0.34) and exhibits an oval outline. This is mainly due to the presence of large prominant bulbous eyes (EDI = 0.15-0.17) which occupy about 75% of the lateral portion of the head. In the earlier

phase the head is partially withdrawn into the mantle cavity. The nuchal cartilage has the same configuration as the adult.

In the adolescent stage the fins are still relatively large although proportionally slightly smaller (FLI = 0.14-0.18 and FWI = 0.36-0.57) than the adult stage. The posterior margin of the late adolescent phase is convex while in the early phase the posterior margin is straight. The anterior margins of both the early and late phases are convex and free lobes are present. The lateral edges of both phases are rounded.

The general condition of the arms in the adolescent stage is similar to the adult stage; however, all the arms are proportionally smaller. The arm formula has changed to II>III>I>IV with arms I = 20-29% of DML, II = 27-41% of DML, III = 23-31% of DML, and arms IV = 16-24% of DML. The lateral longitudinal series of suckers on all arms have the same arrangement and dentition as the adult stage. In the early phase the lateral supporting membranes are weak, indistinct, and discontinuous, while in the later phase these membranes are distinct and continuous. In the late adolescent phase, the median longitudinal rows consist of suckers which are metamorphosing into hooks (Plate 4c); those which have not undergone transformation have from 4-6 teeth on the distal margin of the inner ring. In the early phase the median longitudinal rows are made up of suckers with a dentition of 4-6 teeth.

The tentacles throughout this stage are muscular and proportionally about the same size as the adult stage (TI = 0.45-0.47). The sucker and hook patterns on the tentacle of the late adolescent phase generally

are the same as the adult stage (Plate 4b); however some morphological differences occur. The armature series on the ventral margin of the stalk consists of sucker buds, and the dorsal margin of the stalk has suckers alternating with pads for only a short portion of the distal end. Proximally on the dorsal margin only sucker buds are evident. The dentition of the club suckers is: dactylus 6-8 teeth, ventral marginal zone 8-10 teeth, median zone five teeth and dorsal marginal zone four teeth.

In the early adolescent phase a wide variety of club development can be seen (Plates 5b,c). Generally the central hook is just developing or is evident as a hook bud; there are also fewer suckers and more sucker buds present, and definite sucker bud patterns are evident which closely follow the sucker patterns of the later phase. The locking zone is not developed in the early phase but is fully developed by the late phase. A stalk sucker pattern becomes evident with retrogression from the late to early phases (Plate 5b,c). By the earliest adolescent phase the stalk bears six distinct staggered systematic rows throughout, except at the distal and proximal most portions where the patterns become indistinct. The aboral side of the tentacle in the early phase is covered with large distinct chromatophores. A dorsal lateral keel is present on the dactylus throughout this stage.

The ventral pads of the funnel organ are the same oval shape as in the adult stage. The dorsal pad is V-shaped but is wider than long whereas in the adult stage the opposite is evident. The thickening of the arms of the dorsal pad is not as pronounced and the posterior

sections present a more rounded outline (Plate 4d). In the earlier phase this thickening is evident only as a gradual widening of each arm. The anterior arm ridges are present in the later phase but absent in the early phase. Throughout this stage a long slender papillae is present at the apex of the dorsal pad and the anterior margin is not as distinctly U-shaped. A funnel value is present in both the early and late phases.

Post-Larval Stage

Throughout the post-larval stage the mantle is wide, thin, translucent, weak and very squat in appearance (MWI = 0.56-0.67). The separated epidermis and characteristic chromatophore pattern which existed in the early adolescent phase is also present throughout the post-larval stage (Plate 6a). The free anterior ventral margin has slight projections at the locking cartilage with a barely discernable funnel depression between them. The anterior dorsal margin is straight. The posterior margin tapers abruptly to form a small conical terminus. A small gelatinous tail is present (TaI = 0.05-0.06).

Like the early adolescent phase the head width is greater than its length (HLI = 0.19-0.27 and HWI = 0.28-0.37) and dominated by large bulbous eyes (EDI = 0.14-0.18) which occupy about 75% of the lateral surface of the head. There are usually two to three large distinct chromatophores present on the dorsal surface of each eye and the head is almost completely withdrawn into the mantle cavity.

The fins are proportionally smaller (FLI = 0.09-0.23 and FWI = 0.29-0.51), thin, delicate and oval in appearance. A small free anterior lobe is present and both the anterior and lateral margins are rounded. The posterior margin is also rounded, but to a lesser degree, and projects slightly beyond the tail.

All the arms are relatively short and weak with an arm formula of II>III>I>IV (I = 14-24% of DML, II = 17-31% of DML, III = 15-25% of DML, and IV = 06-14% of DML). The armature of all arms consists of a combination of equal sized suckers and sucker buds. The lateral series are attached to the trabeculae of a weak and discontinuous supporting membrane. There are 2-3 small blunt teeth present on the inner ring of the largest suckers.

The tentacles are relatively large and muscular (TI = 0.39-0.73). The tentacular club is compact and the armature consists entirely of sucker buds (Plate 6b). The dactylus of the late post-larval phase has four distinct rows of sucker buds distally which change to 5-6 rows on the proximal portion. The ventral marginal zone also has four distinct rows of sucker buds which decrease both proximally and distally. Proximally the lateral most row continues onto and terminates on the stalk. Distally the lateral most row of ventral-marginal sucker buds terminates lateral to the central hook bud. There is a small break in the sucker bud pattern lateral to the central hook bud which separates these sucker buds from those of the dactylus. The dorsal-marginal zone has five distinct rows of sucker buds which reduce to three rows proximally and terminate slightly posterior to the median zone sucker buds.

Distally the rows reduce to three distinct series which pass lateral to the central hook bud and merge with the sucker buds of the dactylus. The median zone consists of a distal large hook bud and five proximal sucker buds. Except for the most distal and proximal portions the stalk bears six staggered distinct rows of suckers.

In the early post-larval phase (Plate 6c) similar club sucker patterns can be discerned; however, most of the longitudinal series are incomplete and in some cases it is difficult to determine these patterns. The tentacular stalk of this phase also exhibits six staggered distinct longitudinal rows. Throughout this stage the aboral side of the tentacle is covered with large distinct chromatophores. A weak dorsal lateral keel is present on the dactylus.

The ventral pads of the funnel organ are small and oval in shape. The dorsal pad is V-shaped and approximately twice as wide as long. The arms of the dorsal pad are the same width throughout. The anterior margin is blunt with no indentation and with a papillae originating at the apex. A funnel valve is present.

Larval Stage

The mantle is weak, thin and translucent in preserved specimens (Plate 7a) and presents an extremely rotund appearance (MWI = 0.70-0.79). The anterior portion of the mantle is slightly constricted and both the dorsal and ventral free margins are straight. Posteriorly the mantle constricts abruptly and terminates in a small conical projection. There is a widely separated epidermis which in some cases causes the individual

to appear almost spherical. This epidermis has the same characteristic chromatophore pattern as the post-larval stage. There is a short gelatinous tail present (TaI = 0.03).

The head is short and broad (HLI = 0.16-0.27 and HWI = 0.34-0.45) and totally withdrawn into the mantle cavity. The eyes are large (EDI = 0.14-0.18), protruding, and cover about 75% of the lateral side of the head. The dorsal surface of each eye bears two to three large distinct chromatophores.

The fins are small (FLI = 0.10-0.16 and FWI = 0.30-0.53), delicate, and squarish in outline. There are no free anterior lobes and all the margins are only slightly rounded. The posterior margin extends somewhat beyond the tail.

The arms are all small and weak. The arm formula is II>III=I>IV with arms I = 12-24% of DML, II = 16-34% of DML, III = 12-23% of DML, and arms IV = 5-15% of DML. The armature of arms I-III consists of four longitudinal rows of sucker buds. In all specimens examined there was one or two small developing suckers present at the base of each arm. Arms IV have only three or four sucker buds present at their base; distally the armature is indistinguishable.

The tentacles are large and muscular (TI = 0.57-0.83) with a small, 3% of TL, deltoid shaped club (Plate 7b,c). The oral surface of the tentacles is covered by six distinct staggered rows of suckers. The aboral surface is lined with several large chromatophores.

The dorsal pad of the funnel organ is considerably wider than long and forms a very shallow V-shape. The arms are equal in width throughout

and only a very small papillae is present at the apex. The ventral pads are tiny and round (in many cases the ventral pads were indistinguishable). A funnel valve is present.

Gonatus tinro Nesis, 1972

Adult Stage

The mantle (Plate 8) is moderately thick, muscular, and widest at the anterior margin (MWI = 0.49-0.52). The anterior dorsal magin flares gradually from the lateral edges towards the midline. Small projections are present on the ventral surface at the mantle segment of the funnel-mantle locking cartilage. Between these projections the ventral free margin is slightly emarginated. Posteriorly the mantle tapers gradually to terminate at the conus of the pen. A moderately long tail (TaI = 0.10-0.11) extends posteriorly from the dorsal portion of the mantle terminus.

The fins are moderately large (FLI = 0.33-0.39 and FWI = 0.63-0.71) and muscular. Distinctly sagittal in shape the fin margin are convex anteriorly, concave posteriorly, and sharply rounded laterally. Comparatively small free anterior lobes are present. All surfaces of the mantle and fins are covered with small densely packed chromatophores.

The head is slightly oval in shape (HLI = 0.24-0.28 and HWI = 0.33-0.35) with large eyes (EDI = 0.21) which occupy about 80% of the lateral head surfaces. A distinct anterior sinus is present on each eyelid. An olfactory fold is present on each posterior lateral surface of the head behind the eye. The nuchal cartilage (Plate 9e) is elongated with slightly divergent lateral margins posterior to anterior and with both

the posterior and anterior edges rounded. The cartilage is comparatively stout in appearance, being fairly broad in relation to width.

The arms are moderately long and muscular (I = 40-62% of DML, II = 50-71% of DML, III = 49-71% of DML, and IV = 51-57% of DML) with an arm formula of II≥III≥I≥IV. The armature of arms I-III consists of two lateral series of small suckers and two median series of large sheathed hooks (Plate 9c,d). The lateral suckers are attached to the trabeculae of a strong supporting membrane. The dentition of the lateral suckers is 6-8 short blunt teeth on the inner ring. Arms IV are more slender than arms I-III and possess large lateral keels. The armature of arms IV consists of four longitudinal rows of sucker; the suckers of the median series being are about 1.2 times as large as the corresponding sucker of the lateral series. A supporting membrane is present but is considerably reduced compared with arms I-III. The dentition of the arms IV suckers is 3-5 blunt teeth on the inner ring. All arms are covered with small densely packed chromatophores.

The tentacles are extremely long and slender but muscular (TI = 1.33-1.55). The armature of the club consists entirely of suckers — a unique characteristic for this genus (Plate 9a). The dactylus carries a distal circlet of seven small smooth ringed suckers proximal to which are four longitudinal rows of suckers that increase to eight rows at the base of the dactylus. The manus carries from eight to sixteen longitudinal series of suckers. The dentition of the club suckers is 1-3 short pointed teeth on the anterior portion of the inner ring (Plate 9b). A small dorsal lateral keel is present on the dactylus.

A locking zone is present and consists of a series of 3-4 alternating ridges and grooves. Each ridge carries a large smooth ringed sucker medially and each groove has a large fleshy knob present at its medial edge. The suckers and alternating knobs of this zone are continuous with a dorsal series of alternating suckers and pads on the distal one-half of the stalk. The ventral margin of the stalk has a single series of suckers on the distal one-fourth.

The funnel is relatively small and reaches midway between the posterior edge of the eye and the lens. The funnel locking cartilage (Plate 9f) is lanceolate in shape with a simple straight groove corresponding to a straight cartilaginous ridge on the mantle. The lateral margins of the funnel cartilage are straight and convergent posterior to anterior. A large funnel valve is present.

The dorsal pad of the funnel organ is a deep V-shaped (Plate 9g) with arms which are narrow and slightly broadened posteriorly. There is a slight ridge formation on the anterior segment of the arms and a large prominent papillae present at the apex. The ventral portion of the funnel organ consists of two large flat oval shaped pads.

Adolescent Stage

The mantle (Plage 10c) is generally conical in shape, tapering from a widened anterior margin to a pointed posterior (MWI = .35-.55), and thin but muscular. The anterior free margin is notched on the ventral surface between the projecting mantle locking cartilages.

Posteriorly a long fleshy tail originates from the dorsal posterior margin of the conus (TaI = 0.09-0.10).

The fins are large (FLI = 0.21-0.33 and FWI = 0.55-0.70) and muscular. The lateral edges are rounded and free anterior lobes are present on the convex anterior margin. The posterior margin is nearly straight but is somewhat attenuated along the tail.

The head is slightly oval in shape (HLI = 0.18-0.32 and HWI = 0.31-0.38) with large eyes (EDI = 0.18-0.24) which occupy about 80% of the lateral surface of the head. An anterior sinus is present on each eyelid. A single olfactory fold is present on each posterior lateral surface of the head. Like the adult stage the nuchal cartilage is short and stout with slightly divergent lateral margins.

The arms are moderately long and muscular (I = 30-46% of DML, II = 33-52% of DML, III = 33-51% of DML, and IV = 28-43% of DML). The armature of arms I-III consists of four longitudinal series; two lateral rows of small suckers and two median series of metamorphosing hooks. A continuous strong supporting membrane is present on each lateral series. The dentition of the lateral suckers is 3-5 long blunt teeth on the distal portion of the inner ring.

Arms IV are more slender than arms I-III and carry prominent lateral keels. The armature of these arms consists of four rows of nearly equal sized suckers. The lateral two series are attached to the trabeculae of a weak discontinuous supporting membrane. The dentition of the arm IV suckers is the same as the lateral series on arms I-III.

The tentacles are long, slender and muscular (TI = 0.49-1.55). The armature of the club consists of a combination of suckers and sucker buds with the same arrangement as the adult. In the late phase (Plate 10a) the club is differentiated with a small lateral keel present on the dactylus. The early phase club (Plate 10b) is not differentiated from the stalk and the keel is not present on the dactylus. The dentition of the club suckers is 1-3 short pointed teeth on the anterior portion of the inner ring.

The locking zone of the late phase consists of a series of alternating suckers and fleshy knobs with the corresponding ridges and grooves just becoming distinguishable. The suckers and alterning knobs are continuous with a series of alternating sucker buds and knobs on the dorsal anterior one-half of the stalk. The ventral margin of the stalk has a single series of sucker buds on the anterior one-fourth. The locking zone of the early phase is distinguishable as a small arc of suckers on the dorsal margin of the tentacle. The aboral surface of the stalk is covered with six staggered longitudinal series of tiny suckers.

The funnel is relatively small and reaches midway between the posterior edge of the eye and the lens. The funnel locking cartilage has a simple straight distinct groove and lateral margins which are straight and convergent posterior to anterior. A large funnel valve is present.

The dorsal pad of the funnel organ is a deep V-shaped. The arms are narrow but broaden slightly at the posterior terminus. There is only a hint of ridge formation on the anterior segment of the arms and a large prominent papillae is present at the apex of the dorsal pad. The

ventral portion of the funnel organ consists of two large flat oval pads. A funnel valve is present.

Post-Larval Stage

The mantle (Plate 11b) is thick, muscular, and cylindrical in shape (MWI = 0.24-064). The free anterior margin is straight dorsally but projects slightly at the mantle locking cartilages. A slight funnel depression is present between the ventral projections. The mantle constricts posteriorly to form a blunt terminus at the conus of the pen. A short fleshy tail is present (TaI = 0.03-0.05).

Relatively large (FLI = 0.09-0.20 and FWI = 0.39-0.64) and muscular fins are terminally located on the mantle. The convex posterior margins, extending somewhat beyond the tail, and the rounded anterior and lateral margins impart an oval appearance to the fin. The fin and mantle are sparsely covered with large chromatophores.

The head is large, slightly narrower than the mantle opening, and partially withdrawn into the mantle cavity (HLI = 0.20-0.31 and HWI = 0.30-0.42). Large bulbous eyes (EDI = 0.15-0.32) which cover about 80% of the lateral surfaces dominate the head. The nuchal cartilage is rectangular in shape with rounded anterior and posterior margins. The dorsal surface of the head has one large chromatophore over each eye which in many cases appears to be a composit of two or more smaller chromatophores. Medially this surface supports two additional chromatophores, one at the junction of arms I and another on the midline between

the eyes. The ventral surface supports four chromatophores, one on each eye surface and two on the head surface just medial to each eye.

The arms, with the exception of arms IV, are stout and muscular (I = 27-46% of DML, II = 32-56% of DML, II = 29-51% of DML and IV = 17-37% of DML) with an arm formula of II>III>I>IV. The armature of all arms consists of four series of equal sized suckers, the lateral two series of which are attached to the trabeculae of a greatly reduced and discontinuous supporting membrane.

The tentacles (Plate 11a) are moderately long and stout (TI = 0.41-0.76). The club is short, occupying about 25% of the tentacle length, and covered with small densely packed sucker buds. The oral surface of the tentacular stalk is covered with six staggered rows of small suckers. The aboral surface of the arms and tentacles are covered with a single series of large chromatophores.

The funnel segment of the funnel-mantle locking cartilage is lanceolate with a shallow central groove which is opposed by a straight cartilaginous ridge on the mantle. The dorsal pad of the funnel organ is a shallow V-shape with a slender papillae at its apex. There is a very slight posterior widening of the arms. The ventral portion consists of two oval pads. A funnel valve is present.

Gonatus madokai Kubodera and Okutani, 1977

Adolescent Stage

The mantle wall (Plate 12) is thin, translucent, and somewhat bulbous in shape (MWI = 0.36-0.42); tapering slightly towards the anterior

free margin. The anterior free margin has slight projections at the dorsal midline and on the ventral surface at each of the mantle locking cartilages. Between these ventral projections there is a shallow but distinct funnel depression. Posteriorly the mantle tapers gradually to terminate at the conus of the pen. A short gelatinous tail (TaI = 0.05-0.09) extends posteriorly from the conus. A single series of small dark chromatophores circumscribes the entire anterior margin of the mantle. A second series circumscribes the mantle at the anterior one-fifth and a third series at the midpoint. A single large dark chromatophore is located at the anterior junction of the fin. The remainder of the dorsal, ventral and lateral surfaces are sparsely covered with smaller oval chromatophores.

The fins are large (FLI = 0.32-0.37 and FWI = 0.59-0.64), translucent, and oval in outline. The anterior and lateral margins are rounded and small anterior lobes are present. The posterior margin is straight and even with the posterior tip of the tail. Two large chromatophores are located on the fin directly above the mantle terminus. The remainder of the dorsal and ventral surfaces are covered with small scattered chromatophores.

The head length is greater than the head width (HLI = 0.26-0.30 and HWI = 0.22-0.26) and flattened dorsal-ventrally. The base of the arms is constricted and elongated and surrounded by a thin separated translucent membrane. The eyes are small (EDI = 0.11-0.12), occupying only about 41% of the lateral surfaces of the head. The constricted arm base produces a stalk-like effect on the eyes. The nuchal cartilage

(Plate 13e) is elongate in shape with three longitudinal grooves and corresponding ridges and rounded anterior and posterior margins. The central groove is narrow, deep, and slightly raised, while the two lateral grooves are shallow and wider. There is a single prominent nuchal fold present on each posterior ventral-lateral surface of the head. The dorsal surface of the head has three chromatophores over each eye and a triangular shaped group of three at the base of arms I and II. The ventral surface has a single chromatophore at the junction of arms IV and on each of the ventral surfaces of the eyes.

All of the arms are long and slender but muscular. The arm formula is III=II>I>IV, with arms I = 64-70% of DML, II = 91-96% of DML, III = 93-96% of DML, and IV = 52-55% of DML. Arms III have thin delicate aboral keels and arms IV have small, almost indistinct, lateral keels. The armature of arms I-III consists of two lateral rows of suckers and two median rows of hooks (Plate 13b,c). The lateral two series are attached to the trabeculae of a continuous but greatly reduced supporting membrane. The dentition of the lateral series is 6-8 long pointed teeth on the distal margin of the inner ring. The median two series consist of large heavily sheathed hooks. The armature of arms IV consists of four series of equal sized suckers; the lateral series of which are attached to the trabeculae of a reduced supporting membrane. The dentition of these suckers is 4-6 long pointed teeth on the distal margin of the inner ring.

The tentacles (Plate 13a) are long (TI = 0.91-0.96) and muscular with the club occupying about 25% of the tentacle length. The dactylus

supports a distal circlet of nine small smooth ringed suckers. Proximal to this the dactylus carries four rows of suckers which increases to eight rows at the base. The dentition of these suckers is 6-8 long pointed teeth on the distal margin of the inner ring. A dorsal-lateral keel is present on the dactylus.

The dorsal-marginal zone has six rows of suckers at its widest point. Distally these decrease to four rows which pass lateral to the large central hook and merge with the dorsal suckers of the dactylus. Proximally these rows decrease to one and terminate opposite the last sucker of the locking zone. The dentition of the dorsal-marginal suckers is 4-6 long pointed teeth on the distal margin of the inner ring.

The ventral-marginal zone consists of six longitudinal series of suckers at its widest point. Distally these decrease to two rows which terminate ventral-lateral to the large central hook. The suckers of the ventral-marginal group are not continuous with the suckers of the dactylus and are separated from them by a small gap. Proximally the longitudinal series decrease to two rows which merge with the ventral series of the stalk. The dentition of the ventral-marginal group is 6-8 long pointed teeth on the distal margin of the inner ring.

The locking zone consists of a series of 5-6 large smooth ringed suckers, each of which is situated at the median end of a ridge, alternating with large fleshy knobs, each of which is situated at the median end of a groove. The alternating suckers and knobs are continuous with a series on the dorsal margin of the stalk. The median zone consists of

a developing large central hook preceeded distally by a smaller hook bud and followed proximally by a series of 6-8 smooth ringed suckers.

The armature of the stalk consists of a ventral series of sucker buds which continue for about 75% of the stalk. The dorsal margin supports a series of alternating sucker buds and knobs along the entire dorsal margin. Between the sucker buds of the dorsal and ventral margins are a few scattered suckers which are the remnants of the post-larval armature. Supporting membranes are present along the entire dorsal and ventral margins of the stalk. The ventral membrane is continuous with the ventral marginal trabeculate supporting membrane of the club. The dorsal supporting membrane continues onto the club and terminates on the proximal portion of the dactylus.

The funnel segment (Plate 13d) of the funnel-mantle locking cartilage is lanceolate in shape with a shallow median groove and slightly concave ventral margin. The funnel organ (Plate 13f) consists of a V-shaped dorsal pad and a pair of large oval ventral pads. Posteriorly the arms of the dorsal pad widen abruptly to display distinct shoulders and a trilateral terminus. Each arm has a short weak ridge developing on the anterior portion. There is a long papillae present at the apex of the dorsal pad. A large funnel valve is also present.

Post-Larval Stage

The mantle (Plate 14c) is thin, translucent, and tapers slightly towards the anterior margin; the dorsal portion of which is straight (MWI = 0.33-0.44). The ventral free margin has slight projections at

the mantle segment of the funnel-mantle locking cartilage, between which is a slight funnel depression. Posteriorly the mantle tapers gradually to a pointed terminus at the conus of the pen. A very short gelatinous tail (TaI = 0.01-0.02) extends posteriorly from this terminus. The arrangement of the mantle chromatophores is the same as the adolescent stage.

The fins are large (FLI = 0.14-0.31 and FWI = 0.47-0.61), thin, delicate, and squarish in outline. The anterior and posterior free margins are straight and no anterior free lobes are present.

The arms are still relatively long (I = 32-57% of DML, II = 71-84% of DML, III = 71-84% of DML, and IV = 13-39% of DML), thin, and muscular. The arm formula is II=III>I>IV. In the late phase the armature of arms I-III consists of two lateral rows of suckers and two median rows of hooks which are in various stages of development. The supporting membrane is discontinuous and greatly reduced and in most cases can barely be seen. There is a chromatophore present at the base of each trabeculae of the lateral rows as well as several large chromatophores on the aboral surface of each arm. The dentition of the lateral suckers is six long pointed teeth on the distal margin of the inner ring. The armature of arms IV consists of four rows of sucker buds with a few suckers present at the base of the arms.

The armature of the early phase arms I-III consists of four longitudinal rows of suckers. The lateral suckers are attached to small trabeculae by long peduncles and are about 1.3 times as large as the median suckers. The dentition of the lateral suckers is 2-4 small pointed

teeth on the distal margin of the inner ring. The armature of arms IV consists entirely of four rows of sucker buds.

The tentacles (Plate 14a,b) are thin but muscular and are considerably shorter than the adolescent stage (TI = 0.44-0.66). The club is about 25% of the tentacle length and equiped with sucker buds. In the late phase the arrangement of the sucker buds is the same as the sucker arrangement of the adolescent stage. The early phase armature arrangement cannot be discerned and the club is present as a deltoid area covered with minute sucker buds. The oral surface of the tentacular stalk is covered with five regular alternating rows of small suckers.

The head is squarish in shape (HLI = 0.25-0.28 and HWI = 0.24-0.27) and depressed dorsal-ventrally. The brachial crown is even more tightly constricted than in the adolescent stage. This constriction is covered with a thin separated transparent epidermis and imparts a stalk-like appearance to the eyes. The eyes are small (EDI = 0.11-0.12) and occupy only about 43% of the lateral surface of the head. The nuchal cartilage and funnel cartilage is the same as the adolescent stage only relatively smaller. No nuchal folds are evident.

Larval Stage

The mantle (Plate 15b) is thin, translucent and bulbous in shape (MWI = 0.48-0.86). The mantle tapers slightly anteriorly to a straight free margin. Posteriorly the mantle tapers gradually to a rounded terminus at the conus of the pen.

The fins are small (FLI = 0.05-0.16 and FWI = 0.26-0.39), thin, and delicate. The anterior and posterior margins are rounded giving each fin an oval shape. The fins are attached terminally and the posterior margin extends beyond the terminus of the mantle.

The arms are relatively short (I = 17-29% of DML, II = 34-78% of DML, III = 15-67% of DML, and IV = 04-11% of DML), slender and weak with an arm formula of II≥III>I≥IV. The late phase armature of arms I-III consists of four longitudinal series of suckers which are concordant with the early post-larval phase. The early larval phase armature of these arms consists of four longitudinal series of sucker buds; whereas the armature of arms IV consists entirely of sucker buds throughout this stage.

The tentacles (Plate 15a) are relatively long (TI = 0.70-1.15) and robust with the club consisting of a small, bare area at the distal tip. The oral surface of the stalk is covered with five regular alternating longitudinal series of small suckers.

The head is wider than long (HLI = 0.21-0.28 and HWI = 0.25-0.48) and flattened dorsal-ventrally. The constriction of the brachial crown and the stalk-like appearance of the eyes is even more evident. The eyes are small but larger than in the post-larval stage (EDI = 0.12-0.17) and occupy about 56% of the lateral surfaces. The nuchal cartilage and funnel locking cartilage are the same as the post-larval stage. A funnel valve is present but no nuchal folds are evident.

Gonatus berryi Naef, 1923

Adolescent Stage

The mantle (Plate 16) is thick, muscular, and cylindrical in shape (MWI = 0.35-0.39). The anterior free margin is straight dorsally but projects ventrally at the mantle locking cartilages. Between these projections a shallow but distinct funnel depression is present. Posteriorly the mantle tapers gradually to produce a pointed terminus at the conus of the pen. A relatively long gelatinous tail is present (TaI = 0.10-0.12).

The head is short and wide (HLI = 0.20-0.24 and HWI = 0.31-0.44), with large eyes (EDI = 0.21-0.24) which occupy about 97% of the lateral head surfaces. The nuchal cartilage (Plate 18d) is rectangular with rounded anterior and posterior margins. There are three nuchal folds present on the posterior-lateral surface of the head.

The fins are very large (FLI = 0.39-0.43 and FWI = 0.84-0.87) and muscular with large free anterior lobes present. The posterior margins are slightly concave due to the extension of the fin along the tail.

The arms are moderately long (I = 39-43% of DML, II = 59-61% of DML, III = 60-62% of DML, and IV = 43-46% of DML) and muscular and the arm formula is III>II>I>IV. The armature of arms I-III consists of two lateral series of small suckers and two median series of very large sheathed hooks (Plate 18b). The lateral suckers are attached to the trabeculae of a strong supporting membrane by short stout peduncles. The dentition of the lateral suckers is 6-8 long pointed teeth on the distal margin of the inner ring (Plate 18a). The armature of arms IV

consists of four series of equal sized suckers, the dentition of which is the same as the lateral series of arms I-III. The trabeculae and supporting membrane of the lateral series of arms IV is proportionally reduced.

The tentacles (Plate 17a) are moderately short (TI = 0.49-0.51) but muscular with large clubs, about 49% of the tentacle length. At the tip of the dactylus is a circlet of 12 small smooth ringed suckers. Proximal to this are four regular longitudinal rows of various sized suckers. The size of the suckers decreases both from the base of the dactylus distally and from the dorsal margin ventrally, the largest suckers being located near the dorsal base. There are also several small scattered suckers located ventral to the distal hook of the median zone. The dentition of the dactylus suckers is 8-10 short pointed teeth on the distal portion of the inner ring (Plate 17b).

The armature of the dorsal-marginal zone consists of two rows of suckers. Distally these rows pass lateral to the central hook as two staggered rows and combine with the suckers of the dactylus. The rows decrease to one proximally which terminates medial to the locking zone. The dentition of the dorsal-marginal suckers is 6-8 short pointed teeth on the distal margin of the inner ring (Plate 17f).

The locking zone consists of a series of 6-7 alternating ridges and grooves. Each ridge supports a large smooth ringed sucker at its medial edge (Plate 17c). Located between each sucker and at the medial edge of each groove is a large fleshy knob. At the distal end of the locking zone is a single smooth ringed sucker without a corresponding ridge.

The ventral-marginal zone consists of a lateral group of two longitudinal rows of large suckers and a single medial series of minute suckers. Distally both the large and minute suckers terminate lateral to the large central hook. Proximally the series of minute suckers terminates at the convergence of the manus and stalk but the lateral two series continue proximally to unite with the armature of the ventral-margin of the stalk. The dentition of the large ventral-marginal suckers is 6-8 long pointed teeth on the distal margin of the inner ring (Plate 17c).

The median zone consists of a large central hook preceded distally by a smaller hook. Proximal to the large central hook are two small sucker buds followed by two large suckers. The dentition of the large median zone suckers is eight long pointed teeth on the inner ring (Plate 17d).

The flat oral surface of the stalk supports a single ventral marginal series of suckers which are continuous with the suckers of the ventral-marginal zone of the manus. These suckers are present on the distal one-half of the stalk. On the distal one-third of the dorsal margin are two series of sucker buds which are continuous with the locking apparatus.

The funnel cartilage (Plate 18c) is lanceolate with a slightly concave dorsal margin and slightly convex ventral margin. The funnel organ (Plate 18e) consists of a V-shaped dorsal pad and large paired oval ventral pads. The arms of the dorsal pad widen posteriorly to

produce a flattened cardioform shape. The anterior margin is blunt and a long papillae is present at the apex. A funnel valve is present.

Post-Larval Stage

The mantle (Plate 19a) is thin, muscular, and cylindrical in shape (MWI = 0.12-0.13) with a straight dorsal anterior free margin. Ventrally the free margin projects at the mantle segment of the funnel-mantle locking cartilage, between which is a shallow but distinct funnel depression. Posteriorly the mantle tapers rapidly to a blunt terminus at the conus of the pen. A short gelatinous tail extends posteriorly from the dorsal side of the conus (TaI = 0.02-0.03).

The head is short and wide (HLI = 0.26 and HWI = 0.41-0.45) with large prominent bulbous eyes (EDI = 0.22-0.24) which occupy about 90% of the sides of the head. The nuchal cartilage is rectangular with rounded anterior and posterior margins. Only the deep narrow central groove and corresponding ridge are visible. Nuchal folds are not evident.

The fin is large (FLI = 0.34-0.37 and FWI = 0.68-0.69) and muscular. The rounded anterior margins produce moderately large anterior free lobes. The posterior margin is slightly convex and extends somewhat beyond the terminus of the tail.

The arms are moderately long and muscular (I = 36-38% of DML, II = 41-43% of DML, III = 39-41% of DML, and IV = 20-21% of DML), with an arm formula of II>III>I>IV. The armature of arms I-III is four regular staggered series of suckers and hooks. The lateral two series of small suckers are attached to the trabeculae of a reduced supporting membrane

by stout peduncles. The median two rows consist of large heavily sheathed hooks which are replaced by suckers on the distal tip of each arm. The armature of arms IV consists of four staggered longitudinal series of equal sized suckers with discontinuous and greatly reduced lateral supporting membranes. The dentition of all suckers in this stage is from 4-6 short pointed teeth on the distal margin of the inner ring.

The tentacles (Plate 19b) are relatively short (TI = 0.34-0.35) but muscular with moderately large clubs (36-38% of TL). The armature of the club consists entirely of sucker buds with basically the same arrangement as the adolescent stage. The distal tip of the dactylus is bare followed proximally by four longitudinal rows of sucker buds. At the base of the dactylus these four rows divide with the dorsal two merging with the suckers of the dorsal-marginal group and the ventral two terminating lateral to the distal hook buds of the median zone.

The dorsal-marginal zone consists of two series of sucker buds which terminate proximally medial to the developing locking zone. Distally the rows pass laterally to the large central hook and merge with the sucker buds of the dactylus.

The locking zone consists of a series of 4-5 sucker buds on the lateral most edge of the dorsal margin. The accompanying ridges, grooves, and freshy knobs have not yet begun to develop.

The ventral marginal zone consists of two longitudinal series of suckers buds which terminate distally lateral to the large central hook bud and proximally at the base of the manus. About midway along the

ventral-marginal group are two dorsally projecting loops of sucker buds. The dorsal most loop consists of the proximal median zone armature connected to the ventral-marginal zone armature by two sucker buds. The ventral most of these loops, consisting of five sucker buds, rejoins the ventral-marginal sucker buds near the proximal terminus.

The median zone consists of an extremely large central hook bud preceded distally by a smaller hook bud. The proximal portion of the median zone consists of a series of five sucker buds which are connected at the distal end with the buds of the ventral-marginal zone.

The flat oral surface of the tentacular stalk is covered with small suckers. Proximal to the club are 6-8 irregular rows of densely packed suckers. These are followed proximally by five regular staggered series of suckers. Near the base of the tentacle these decrease to 1-2 rows and terminate.

The funnel segment of the funnel-mantle locking cartilage is lanceolate in shape with a slightly concave dorsal margin and slightly convex ventral margin. The funnel organ consists of a small V-shaped dorsal pad and two oval ventral pads. There is no apparent widening of the arms. A long papillae is present at the apex. A funnel valve is present.

Gonatus sp. (Probable new species)

Adult Stage

The mantle is thin but muscular and conical in shape (MWI = 0.33-0.35), tapering gradually from the anterior free margin to the conus of

the gladius (Plate 20). The anterior free margin projects slightly at the dorsal midline and at the mantle segments of the funnel-mantle locking cartilage. The ventral margin is shallowly notched between the ventral projections. A long tail (TaI = 0.15-0.16) extends posteriorly from the terminus of the mantle musculature. All surfaces of the mantle and fins are covered with small reddish-brown chromatophores.

The fins are relatively small (FLI = 0.41-0.45 and FWI = 0.52-0.53), thin but muscular, and distinctly sagittal in shape. Small free lobes are present on the convex anterior portion. Attenuation of the fin along the tail produces a concave posterior margin.

The head width is greater than head length (HLI = 0.23-0.24 and HWI = 0.35-0.36) and dominated by large eyes (EDI = 0.18) which cover about 80% of the lateral surfaces. The nuchal cartilage (Plate 22d) is elongated with a rounded anterior edge and lateral margins which taper slightly to a rounded posterior margin. The cartilage bears the normal configuration of ridges and grooves. One nuchal fold is present.

All the arms are strong and muscular with an arm formula of II>III>IV>I (arms II = 63-65% of DML, III = 57-58% of DML, IV = 54-57% of DML, and arms I = 45-49% of DML). Arms IV have small lateral keels. The armature of arms I-III consists of two lateral series of small suckers and two median series of large sheathed hooks (Plate 22a,b). The lateral suckers are attached to the trabeculae of a weak supporting membrane by short peduncles. The dentition of these suckers is 6-8 teeth on the inner ring. The median rows of hooks are replaced by suckers at the distal tips. The armature of arms IV consists entirely of suckers.

The suckers of the lateral series have the same arrangement and dentition as those of the lateral series of arms I-III; however, the supporting membrane is discontinuous and not pronounced. The median rows of suckers are 1.3 times as large as the lateral series and have a dentition of 8-10 long pointed teeth.

The tentacles are long (TI = 0.87-0.90) and muscular with small complex clubs (25% of TL) which support the typical sucker bearing zones of the genus (Plate 21a). The suckers on the dactylus consist of four series with the largest suckers on the proximal dorsal border. The sucker size decreases both toward the ventral border and distally, near the distal tip all the suckers are approximately the same size. Proximally the four longitudinal series are difficult to distinguish. The dorsal two rows in this area are large and systematic while the ventral two are small and scattered. At the base of the dactylus there are several small suckers which lie on the ventral-lateral side of the central hooks and are separated from the suckers of the dactylus by a small bare area. In smaller adult specimens these suckers are not distinctly separated from the dactylus suckers nor is the sucker size distinction as evident. A trabeculate protective membrane is present on the entire ventral border of the dactylus. The dentition of the larger suckers is 8-10 long pointed teeth (Plate 21b) and that of the smaller suckers is 6-8 shorter blunter teeth.

The ventral-marginal zone supports four longitudinal series of suckers, three rows of large lateral suckers and one row of minute median suckers. Occasional minute suckers are situated between the

median series and the three lateral rows which may be the rudiments of a fifth series. The median row of minute suckers terminates distally lateral to the large central hook and proximally posterior to the median zone. The three lateral rows of large suckers decrease to one series proximally but there is no reduction distally. Distally the initial set of suckers are much smaller than the rest of the suckers in the series; however, they are larger than the minute median suckers. Proximally the lateral most series continues onto the stalk and terminates on the distal one-sixth of the stalk. The dentition of the ventral-marginal zone suckers is 6-8 long pointed teeth in the lateral series (Plate 21c) while the minute suckers are smooth ringed. All the suckers are attached to trabeculae of a strong supporting membrane by long stout peduncles.

The dorsal-marginal zone supports four longitudinal series of suckers at its widest point. Distally these decrease to three rows which pass lateral to the large central hook. At the junction of the dorsal-marginal zone and the dactylus there is a single set of two large suckers. Proximally the longitudinal series decrease rapidly to one row which terminates opposite the last hook in the median zone. The dentition of the dorsal-marginal zone suckers is 5-7 short pointed teeth on the distal portion on the inner ring (Plate 21e).

The locking zone consists of six alternating grooves and ridges. There is a large smooth ringed sucker (Plate 21f) at the medial end of each ridge and a fleshy knob recessed at the median edge of each groove. The distal most groove and ridge are indistinct. Proximally the musculature of the locking apparatus ends abruptly and is connected to the

stalk by a supporting membrane between the termination of the locking apparatus and the distal portion of the stalk. On the distal portion of the stalk proximal to and continuous with the suckers of the locking zone is a series of alternating smooth ringed suckers and pads. This series continues the entire length of the dorsal margin of the stalk.

The distal most portion of the median zone is comprised of an extremely large central hook and a much smaller distal hook. Proximal to these hooks are five small sheathed hooks (Plate 21d). The size of the proximal series of hooks decreases both distally and proximally, the largest hook being the central one.

The funnel is large and extends considerably from the mantle. The funnel locking cartilage (Plate 22c) is ventrally convex and dorsally concave. The mantle segment of the locking cartilage is a straight cartilaginous ridge. The dorsal pad of the funnel organ is V-shaped, each arm of which widens near the posterior to produce a cardioform terminus. The anterior segment of each arm carries a median longitudinal ridge which continues to the apex. In the center of the blunt anterior margin a single, long, slender papillae originates. The ventral pads are cardioform with a blunt anterior margin and a pointed posterior margin. A large funnel valve is present.

Adolescent Stage

The mantle (Plate 23c) is thin, muscular, and cylindrical in shape (MWI = 0.42-0.45). Anteriorly the mantle projects at the dorsal midline and ventrally at the funnel locking cartilages. The mantle is slightly

emarginated between the locking cartilages. Posteriorly the mantle tapers gradually to terminate at the conus of the pen. A small short fleshy tail (TaI = 0.03-0.04) extends from the termination of the mantle to the posterior border of the fin. All surfaces of the mantle and fins are sparsely spotted by chromatophores.

The fins are large and muscular (FLI = 0.13-0.35 and FWI = 0.43-0.87). The margins are anteriorly convex, laterally rounded, and posteriorly straight. Free anterior lobes are present.

The head width is greater than head length (HLI = 0.22-0.24 and HWI = 0.27-0.34) with large prominent eyes (EDI = 0.15-0.21) that cover about 80% of the lateral surfaces of the head. The nuchal cartilage has the same configuration as the adult. One nuchal fold is present. The dorsal and ventral surfaces of the head are spotted with chromatophores.

The arms are moderately long (I = 31-47% of DML, II = 37-59% of DML, III = 31-55% of DML, and IV = 26-47% of DML) and muscular with an arm formula which has changed to II>III≥I>IV. The armature of the arms consists of four rows of suckers of which the lateral suckers have 7-8 short blunt teeth and the median suckers have 6-8 long pointed teeth on the distal margin of the inner ring. A continuous but reduced supporting membrane is present along each lateral series of suckers. Each sucker of the median two rows is about 1.2 times as large as the corresponding lateral sucker. Small lateral swimming keels are present on arms IV and the trabeculae and supporting membrane of these arms are greatly reduced.

The tentacles (Plate 23a,b) are moderately short (TI = 0.37-0.49) and muscular with large complex clubs (about 49% of TL). Distally the tip of the dactylus has a circlet of twelve small smooth ringed suckers which is followed proximally by four longitudinal series of suckers. Unlike the adult there is little difference in size between the dorsal and ventral series. The proximal portion of the dactylus has two transverse rows of five suckers.

The dorsal-marginal zone consists of four longitudinal rows at its widest point. Distally these pass lateral to the large central hook in two to three irregular rows and merge with the suckers of the dactylus. Proximally the series reduce to one which terminates medial to the locking zone. The dentition of these suckers is 5-7 teeth on the distal portion of the inner ring.

The ventral-marginal zone consists of three longitudinal series of suckers, which decrease in size both distally and medially, with an occasional fourth series of minute suckers medial to these. Proximally the series decreases in number to become a single row of sucker buds along the ventral margin of the stalk. These sucker buds terminate on the distal one-half of the stalk.

The locking zone consists of five alternating grooves and ridges. At the median edge of each ridge lies a large smooth ringed sucker and each groove terminates medially in a large fleshy knob. Distally the locking apparatus terminates at a large smooth ringed sucker without a corresponding ridge. Proximally the locking apparatus continues onto

the dorsal margin of the stalk as initially a series of suckers alternating with fleshy knobs and finally as a series of sucker buds. This dorsal series is evident along the entire dorsal margin of the stalk. The median zone consists of a developing large central hook and a distal hook bud. Proximal to these are a single series of three to five suckers.

The club of the early phase of this stage (Plate 23b) has basically the same arrangement of suckers and hooks as the late phase, the differences being that the ventral-marginal zone consists of only three rows of sucker buds and does not show a fourth medial row, the dorsal and ventral marginal series on the stalk are not evident and the ridges and grooves of the locking zone are not prominent. The stalk of this phase carries five alternating longitudinal rows of suckers throughout its length.

The funnel locking cartilage and the funnel organ are basically the same as the adult. In this stage, however, the ridges are not evident on the arms of the dorsal pad of the funnel organ.

Post-Larval Stage

The mantle (Plate 24c) is thin walled, muscular and cylindrical in shape (MWI = 0.35-0.61). The dorsal free margin is straight but ventrally there are slight projections at the mantle locking cartilages and an emargination between them. Posteriorly the mantle constricts rapidly to a pointed terminus at the conus of the pen. There is no gelatinous

tail evident and the terminus of the mantle corresponds with the posterior edge of the fin. The fins are moderate in size (FLI = 0.07-0.31 and FWI = 0.24-0.54), thin, translucent and oval in shape. There are small free anterior lobes present. A few sparsely placed chromatophores are present on all surfaces of the mantle and fins.

The head is considerably wider than long (HLI = 0.19-0.33 and HWI = 0.30-0.44) with large bulbous eyes (EDI = 0.14-0.22) which cover about 70% of each side of the head. The dorsal surface of the head has five large chromatophores, two located over each eye and one located medially. The ventral surface has one chromatophore over each eye and another smaller chromatophore located at the confluence of arms IV.

The arms are moderate in length and muscular (I = 19-59% of DML, II = 23-55% of DML, III = 21-46% of DML, and IV = 12-27% of DML) with an arm formula of II>III≥I>IV. The armature of all arms consists of four longitudinal series of equal sized suckers. The lateral two series are attached to trabeculae but no supporting membrane is evident. The aboral surface of each arm has a single series of large chromatophores.

In this stage the tentacles (Plate 24a,b) are long (TI = 0.41-0.75) and muscular. The club is large (about 45% of TL) and covered with sucker buds. In the late phase the arrangement of the sucker buds on the dactylus is the same as the adolescent stage. The distal circlet is missing but proximal to this area are four longitudinal series. At the base of the dactylus are two transverse series of five buds.

The dorsal-marginal group consists of four longitudinal series which decrease distally to two or three series. Proximally the rows

decrease to one which terminates opposite the developing locking zone. The arrangement of sucker buds on the ventral-marginal zone is three rows which decreases both distally and proximally to one row.

The median zone consists of a large prominent central hook bud with a smaller distal hook bud. Proximal to the central hook bud is a series of three to four sucker buds. The locking zone consists of a series of five to seven sucker buds. There is no indication of the development of the accompanying grooves and ridges.

The early phase of this stage exhibits a club with a central hook bud evident and scattered sucker buds over the oral surface. All phases of this stage have five staggered rows of suckers along the oral surface of the stalk. The aboral surface of the tentacles of this stage have a longitudinal series of large dark chromatophores.

Larval Stage

The mantle (Plate 27c) is thin but muscular. It is widest at the posterior one-third and tapers slightly toward the anterior and abruptly toward the posterior (MWI = 0.51-0.79). The dorsal and ventral anterior free margins are straight. The blunt posterior terminus of the mantle corresponds with the conus of the pen. There is no tail evident. The mantle is sparsely spotted with chromatophores.

The fins are small (FLI = 0.08-0.15 and FWI = 0.26-0.36) and delicate. The margins are rounded giving the fins an overall oval shape. The posterior edges of the fins are slightly extended beyond the termination of the mantle. Each fin has a single dark chromatophore at the base.

The arms are moderately long (I = 19-41% of DML, II = 29-53% of DML, III = 20-45% of DML, and IV = 6-30% of DML) but weak and the arm formula is II≥III≥I>IV. The armature consists of four rows of sucker buds in the early phase and four rows of equal sized suckers in the late phase. Each aboral surface carries a series of large chromatophores.

The tentacles (Plate 25a,b) are moderately large (TI = 0.46-0.77) and muscular. The club is visible as a small bare area at the distal tip of the tentacle. The oral surface of the stalk is covered by five regular staggered rows of suckers. A single series of large dark chromatophores spot the aboral surface.

Gonatus pyros Young, 1972

Adult Stage

The mantle of the single speciman is muscular, narrow (MWI = 0.30), and widest at the anterior margin (Plate 26). Posteriorly the mantle tapers gradually with the musculature terminating in a long slender point at the conus of the pen. A long gelatinous tail (TaI = 0.15) extends posteriorly from the dorsal apex of the conus. There is no projection at the dorsal midline of the anterior free margin; however, ventrally the free margin projects at the mantle locking cartilages. Between these projections is a sharp, deep funnel depression.

The fins are large (FLI = 0.48 and FWI = 0.75) and muscular with large free anterior lobes. The posterior margin is slightly concave due to the attenuation of the fins along the tail. The anterior and lateral margins are convex and sharply rounded respectively.

The head is wider than long (HLI = 0.20 and HWI = 0.30) and squarish in shape with a distinct funnel depression in the ventral surface. The posterior ventral surface of the head is covered with a silver-white reflective type membrane. This membrane was damaged in both specimens examined and therefore the full extent of this membrane could not be determined. The eyes are relatively large (EDI = 0.21), covering about 70% of the lateral surface of the head, with a large oval shaped photophore present on the ventral surface. The nuchal cartilage (Plate 28d) is rectangular with rounded anterior and posterior margins. There is a single nuchal fold present on each posterior lateral surface of the head.

The arms are long and muscular (I = 58% of DML, II = 65% of DML, III = 76% of DML, and IV = 70% of DML) and exhibit the same quadraserial armature as other members of this family. Arms I, II, and III have two median series of large sheathed hooks and two lateral series of small suckers. The suckers are attached to the trabeculae of a strong supporting membrane by stout peduncles. The dentition of the lateral suckers is 6-8 long pointed teeth on the distal margin of the inner ring. Arms IV have four rows of suckers, the lateral of which are attached to long trabeculae by short peduncles. The dentition of the lateral series is 6-8 long pointed teeth. The median two series of suckers are slightly larger (about 1.2 times) than the lateral rows and are attached by long peduncles. The dentition of these suckers is also 6-8 long pointed teeth. A supporting membrane is present along each of the lateral series;

however, this membrane is not as pronounced as on the other sets of arms. Small lateral keels are present on arms IV.

The tentacles (Plate 27a) of this species are long (TLI = 0.73) with moderately short clubs (30% of TL) which have the complex structure typical of this genus. The dactylus supports a distal tip circlet of eight small smooth ringed suckers, followed proximally by four systematic densely packed longitudinal rows of suckers which increase in size from the distal tip. At the base of the dactylus these rows increase to six longitudinal series. The dentition of these suckers (Plate 27b) is 4-6 short blunt teeth on the inner ring. There is a trabeculate supporting membrane along the entire ventral margin. A dorsal lateral keel is present.

The dorsal-marginal zone supports four rows of suckers at its widest part. Distally these rows decrease to one set of two which lie directly lateral to the large central hook and then increase to three and merge with the suckers of the dactylus. Proximally the dorsal-marginal series decreases to one row which terminates opposite the last proximal hook of the median zone. The dentition of these series is four long slender pointed teeth on the distal margin of the inner ring (Plate 27c).

The locking zone consists of five alternating ridges and grooves. Each ridge has a large smoothed ringed sucker at its median edge (Plate 27e) and each groove has a fleshy knob recessed at its median margin. There is a single small smooth ringed sucker on the distal end of the zone without a corresponding ridge.

The ventral-marginal zone supports four longitudinal series at its widest point. Distally these rows decrease to one set of two which lie ventral lateral to the large central hook. There is a distinct break between these suckers and the suckers of the dactylus. Proximally the ventral-marginal suckers decrease to one series which is continuous with the suckers on the ventral margin of the stalk. Each sucker in this zone is attached to strong trabeculae which originate in the median zone of the club. The dentition of these suckers is 4-5 short pointed teeth on the distal margin of the inner ring (Plate 27f).

The armature of the median zone consists of a large central hook preceded distally by a smaller hook. Proximal to the large central hook is a series of three small hooks. The size of the hooks in this proximal series increases toward the large central hook.

The dorsal margin of the stalk has a pseudo-locking zone arrangement on the distal one-fifth. Though not as pronounced as in the locking zone, the ridges with median suckers and the grooves with median knobs are evident. This arrangement is followed proximally by a series of alternating suckers and pads. The ventral margin supports a single series of suckers with several scattered suckers medial to this series. There is a supporting membrane along the entire ventral margin of the stalk. On the aboral surface of the stalk there is a silver-white irridophore which extends from the base distally about one-fourth of the length of the stalk.

The funnel locking cartilage (Plate 28c) is the straight groove and ridge typical of the genus. The dorsal side of the funnel segment is slightly concave and the ventral margin slightly convex. The funnel

organ (Plate 28e) consists of a V-shaped dorsal pad and two oval ventral pads. Each arm of the dorsal pad supports a distinct ridge on the anterior portion and posteriorly widens abruptly to form distinct shoulders. At the apex of the dorsal pad a long slender papillae is present.

Gonatus Type A (Probably *kamtschatica*)

Adolescent Stage

The mantle (Plate 31) is cylindrical in shape, narrow (MWI = 0.28-0.36), thick, and muscular. The anterior free margin flares outward from the lateral edges towards the midline and projects at the mantle locking cartilages. Between the ventral projections is a deep, distinct funnel depression. The posterior one-third of the mantle tapers gradually to terminate at the conus of the pen. A moderately long tail (TaI = 0.05-0.06) extends from the dorsal margin of the mantle terminus. The dorsal and lateral surfaces of the mantle are covered by moderately large oval shaped chromatophores. Two very large dark chromatophores are present on the dorsal midline, one at the anterior one-eighth and another midway along the mantle. The ventral surface is sparsely covered with smaller chromatophores. A series of tiny dark chromatophores is located along the anterior margin and another more posterior series of five larger dark chromatophores is present about one-eighth of the mantle length from the anterior margin.

The head is squarish in outline and nearly as wide as long (HLI = 0.19-0.23 and HWI = 0.17-0.21) with moderately large eyes (EDI = 0.11-0.12), occupying about two-thirds of the lateral surfaces. The head is

severely depressed dorso-ventrally and a distinct ventral indentation is formed between the eyes. There is one large nuchal fold present on each posterior lateral surface of the head. The nuchal cartilage (Plate 30f) is elongated with rounded anterior and posterior margins.

The fins are large (FLI = 0.21-0.27 and FWI = 0.33-0.49) and muscular. Each fin is anteriorly convex and posteriorly concave with sharply rounded lateral margins. Large anterior lobes are present.

The arms, arm formula II>III>I>IV (I = 29-38% of DML, II = 37-47% of DML, III = 34-46% of DML, and IV = 17-30% of DML), are muscular and possess the armature pattern typical of the family. The lateral two rows of suckers (Plate 30d) are attached to the trabeculae of the supporting membrane by long peduncles. The supporting membrane is continuous, but weak and reduced. The median two rows of arms I-III consist of a combination of suckers and metamorphosing hooks (Plate 30c). The lateral suckers are 1.5-2 times as large as the corresponding median sucker. The dentition of the arm suckers is 5-6 short pointed teeth on the distal margin of the inner ring. The armature arrangement of arms IV is similar to the other arms; however, the supporting membrane is discontinuous, evident only along the trabeculae, and much weaker. The dentition is the same as arms I-III.

The tentacles (Plate 30a,b) are relatively short (TI = 0.39-0.43) with a comparatively large club, about 50% of the tentacle length. The armature of the earlier phases generally exhibits the same patterns as those of the later phases; however, there are fewer suckers and more sucker buds present. The dactylus is long and slender and makes up

about 65% of the club length. The armature of the dactylus consists of four longitudinal series of suckers at the distal tip which quickly increase to five rows. The number of rows continues to increase and reaches between eight and ten at the base of the dactylus. There is no circlet present at the distal tip of the dactylus.

The armature of the dorsal-marginal zone consists of four longitudinal series of suckers which decrease to three and pass lateral to the large central hook bud. Distally the rows of the dorsal-marginal zone merge with the suckers of the dactylus. Posteriorly the suckers of this region decrease to one row and terminate opposite the last sucker of the locking zone.

The ventral-marginal zone supports five longitudinal rows of suckers at its widest point. Distally these rows decrease to one which terminates opposite the small distal median zone hook bud. The armature of this region is discontinuous with the suckers of the dactylus. Proximally the rows also decrease to one which is continuous with a row of ventral marginal sucker buds on the stalk. In the earlier phase of this stage the armature of this region terminates proximal to the median zone.

The locking zone consists of a series of five large sucker buds, each of which is situated at the median end of a ridge. Between each primary ridge there is a secondary ridge without a sucker which is separated by distinct narrow grooves and which terminates in the median musculature of the manus. There is no evidence of the fleshy knobs which are present on the locking zone of other members of this genus.

The distal most sucker of this zone does not have a corresponding ridge. Proximally the ridges and suckers of the locking zone are continuous with a series of suckers and sucker buds along the dorsal margin of the stalk. The locking zone of the early phase consists of a series of sucker buds along the dorsal margin. There is no evidence of the development of the corresponding ridges or fleshy knobs. The median zone consists of a large central hook bud and a smaller distal hook bud. Proximal to these hook buds are a series of six suckers or sucker buds.

In the late phase the stalk supports a ventral series of sucker buds that is continuous with the ventral-marginal zone and a dorsal series of buds that is continuous with the sucker buds of the locking zone. The most distal three members of the dorsal series exhibit the same structure as those of the locking zone. Situated between the two marginal series are several scattered suckers that are remnants of the earlier phase armature. In the earlier phase the dorsal and ventral series are not present. On the distal most portion of the stalk there are four regular regimented series of suckers. Proximal to this the armature converts to four longitudinal series of staggered suckers which are continuous to the proximal portion of the stalk where they decrease in number and terminate.

In both the early and late phase there is a supporting membrane present on the dorsal and ventral margins of the stalk. The ventral supporting membrane continues onto the club and is present along the entire length of the ventral-marginal zone and the dactylus. The dorsal supporting membrane also continues onto the club and is present

along the entire length of the dorsal-marginal zone. This supporting membrane terminates on the proximal portion of the dactylus.

The funnel locking cartilage (Plate 30e) is a straight groove and ridge. The funnel segment is lanceolate with a slightly concave dorsal margin. The mantle segment is a straight ridge which flares somewhat posteriorly. The funnel organ (Plate 30g) consists of a V-shaped dorsal pad and two oval ventral pads. The arms of the dorsal pad are narrow and rounded with a slight widening and flattening in the proximal portions. There are no distinct shoulders or ridges present on the arms. A long slender parillae is present at the apex of the dorsal pad. A large funnel valve is also present.

Post-Larval Stage

The mantle (Plate 31) is cylindrical in shape and though slightly wider than the adolescent stage is still comparatively narrow (MWI = 0.29-0.37). The anterior free margin has projections at the dorsal midline and the mantle locking cartilages. A deep funnel depression is located between the ventral mantle projections. Posteriorly the mantle tapers gradually to a conical terminus at the conus of the pen. A short gelatinous tail (TaI = 0.02-0.03) extends from the posterior mantle terminus. The mantle chromatophore pattern is similar to the adolescent stage; three large oval dark chromatophores located on the dorsal midline: one at the anterior one-fifth and two just posterior to the midpoint. The remainder of the dorsal and lateral surfaces of the mantle are covered with a moderate number of smaller chromatophores.

The ventral surface of the mantle is sparsely covered with small oval chromatophores. A single series of dark oval chromatophores is present near the anterior one-fifth and another series of tiny chromatophores is present around the entire anterior margin.

The fins are relatively small and weak (FLI = 0.18-0.31 and FWI = 0.33-0.55). The anterior margins are sharply convex and large free anterior lobes are present. The lateral and posterior margins are gently rounded and straight respectively. A series of chromatophores is present along both the dorsal and ventral posterior margin of the fin. Only a few scattered chromatophores are present over the remainder of the two surfaces.

The head is squarish in shape (HLI = 0.14-0.23 and HWI = 0.19-0.24) and partially withdrawn into the mantle cavity. The eyes are relatively small (EDI = 0.11-0.14) and occupy only about one-half of the lateral surfaces. The eyes protrude ventrally and produce a concavity in the ventral surface of the head. There is a single distinct chromatophore on the ventral surface of each eye while the dorsal surface of the head has six large chromatophores, three over each eye. A nuchal fold is present on each posterior ventral-lateral surface. The nuchal cartilage (Plate 32f) is rectangular with rounded anterior and posterior margins and the normal configuration of ridges and grooves.

The arm formula is II=III>I>IV with arms IV considerably smaller than the others (I = 17-35% of DML, II = 27-46% of DML, III = 28-43% of DML and IV = 6-21% of DML). The armature of all arms consists of four longitudinal series of suckers. The lateral series of arms I-III are

attached to short thick trabeculae by stout peduncles. The supporting membrane is discontinuous and is only evident as small fleshy ridges on the trabeculae. The size of the suckers increases from the base to the middle of the arm and then decreases towards the distal tip. The suckers in the lateral series are about 1.5 times the size of the corresponding median row of sucker (Plate 32c,d). The dentition of the lateral suckers is 6-8 short pointed teeth on the distal portion of the inner ring and the dentition of the median suckers is 4-6 short blunt teeth on the distal portion of the inner ring. The distal tip of each arm is covered with small sucker buds.

The tentacles (Plate 32a,b) are shorter than the longest arms but stout and muscular (TI = 0.42-0.50). Unlike the adolescent stage the club is short and compact and covered with minute closely packed sucker buds. The central hook bud is evident but is not large. The distal most portion of the stalk has four regimented series of suckers followed proximally by four staggered rows. There is a supporting membrane present on both the dorsal and ventral margins of the stalk. The aboral surface of the tentacle is covered with a series of large distinct chromatophores.

The funnel segment of the funnel-mantle locking cartilage (Plate 32e) is lanceolate with a slightly concave dorsal margin. The mantle segment is a straight ridge. The funnel organ (Plate 32g) consists of a dorsal V-shaped pad and two oval ventral pads. The dorsal pad widens along each arm and has a long papillae present at the apex. A funnel valve is present.

Larval Stage

The mantle (Plate 33b) is thin, translucent, weak, and relatively narrow (MWI = 0.39-0.50). The anterior portion of the mantle is cylindrical, while posteriorly the mantle tapers rapidly to terminate at the conus of the pen. A very short tail (TaI = 0.01-0.02), protrudes beyond this point. The dorsal anterior free margin is straight while the ventral margin has a shallow funnel depression, but no projections at the mantle segment of the funnel-mantle locking cartilage. Both the dorsal and ventral surfaces of the mantle are sparsely covered with small chromatophores.

The fins are comparatively smaller than the post-larval stage (FLI = 0.09-0.27 and FWI = 0.31-0.47), thin, and delicate. The anterior margins are slightly rounded producing small anterior free lobes. The posterior margin is straight and does not extend beyond the tail. Small chromatophores sparsely cover the dorsal and ventral surfaces of the fins.

The arms are small and weak. The arm formula is II = III≥I>IV with arms I = 19-31% of DML, II = 37-41% OF DML, III = 21-43% of DML, and arms IV = 12-14% of DML. All the arms are covered orally with four alternating series of sucker buds and aborally with a single series of large dark chromatophores.

The tentacles (Plate 33a) are moderately large (TI = 0.37-0.65), thick, and muscular. The tentacles are rod shaped but flare somewhat on the distal oral surface. This enlarged area carries four systematic

series of suckers preceded distally by a small sucker free tip. Proximally the tentacle carries four staggered longitudinal series of suckers which are continuous to the base where they decrease to one row and terminate. The aboral surface carries a single series of several large dark chromatophores.

The funnel locking cartilage is lanceolate in shape with a single very shallow and indistinct longitudinal groove. The funnel organ consists of a V-shaped dorsal pad and two oval ventral pads. There is a papillae present at the apex of the dorsal pad. A funnel valve is also present.

Genus *Berryteuthis* Naef, 1923

Berryteuthis anonychus Pearcy and Voss, 1969

Adolescent Stage

The mantle musculature is thick and strong. The shape of the mantle is narrow (NWI = 0.30-0.37) and cylindrical with the posterior portion tapering to a point at the conus of the pen (Plate 34). Anteriorly the free margin projects slightly at the dorsal midline and ventrally at the locking cartilage. There is a sharp, deep, and distinct funnel depression on the ventral surface between the locking cartilages. A short barely discernable gelatinous tail (TaI = 0.02-0.05) projects posteriorly from the mantle terminus. The mantle is moderately well covered with small reddish-brown chromatophores.

The fin is small (FLI = 0.19-0.24 and FWI = 0.34-0.45), generally oval in shape, thick, and muscular. The margins are anteriorly convex,

laterally rounded, and posteriorly slightly concave. Free anterior lobes are present and the dorsal and ventral surfaces are sparsely covered with small chromatophores.

The head is squarish in shape (HLI = 0.21-0.28 and HWI = 0.21-0.30) with moderately large eyes (EDI = 0.12-0.16) that cover about 60% of the lateral surfaces. The head is depressed dorso-ventrally and the eyes extend somewhat below the ventral surface imparting a slight concavity to this surface. The nuchal cartilage (Plate 35c) is distinctly panduraform in shape with sharply rounded anterior and posterior margins. One discernable nuchal fold is present on each posterior lateral surface of the head. The dorsal surface of the head is sparsely covered with moderate sized chromatophores. The ventral surface has a dark distinct chromatophore on each eye, two large chromatophores medial to these and a few small scattered chromatophores covering the remainder of this surface.

The arms are short, stout, muscular, and nearly equal in length. An arm formula of II>III>I≥IV is the most commonly observed with arms I = 24-36% of DML, II = 27-41% of DML, III = 25-40% of DML, and arms IV = 21-33% of DML. The armature of all arms consists of four longitudinal series of suckers. The lateral two series of smaller suckers (Plate 35d) are attached to the trabeculae of a weak discontinuous supporting membrane. The median two series of suckers are 1.2-1.3 times the size of the corresponding lateral sucker (Plate 35c). The dentition of the lateral series is 3-4 long blunt teeth while the median series has 4-6 long blunt teeth on the inner ring. A single chromatophore

extends onto the oral surface from the anterior base of each trabeculae in the lateral series. Each chromatophore passes the posterior base of a median sucker and reaches the midline of the oral surface. The aboral surface of each arm carries a single series of large chromatophores.

The tentacles (TI = 0.24-0.57) are strong and muscular with only a slightly differentiated club area. In the late phase the anterior one-half of each tentacle is covered with minute densely packed sucker buds (Plate 35a) which are arranged in four longitudinal series at the distal tip of the dactylus and increase to 10 rows at the confluence with the manus. The manus supports from 10 to 18 rows of densely packed sucker buds. In the early phase (Plate 35b) there is no detectable arrangement of either the scattered sucker buds which cover the club area or the scattered suckers on the stalk.

A thin delicate dorsal-lateral keel is present on the dactylus of the late phase and is absent in the early phase. The aboral surface of both phases is spotted with a series of large dark chromatophores and a few smaller scattered chromatophores.

The funnel segment of the funnel-mantle locking cartilage (Plate 35f) is lanceolate in shape with a distinct medial groove. The mantle segment is a straight ridge which flares slightly toward the posterior. The funnel organ (Plate 35g) consists of an elongated U-shaped dorsal pad and two large tear-drop shaped ventral pads. The arms of the dorsal pad are thick and approximately the same width throughout. Each arm flattens at the posterior terminus. A short thick papillae is present at the anterior apex of the dorsal pad.

Berryteuthis magister Berry, 1913

Adult Stage

The mantle (Plate 36) is thick, muscular, and anteriorly cylindrical in shape (MWI = 0.30-0.42). With the dorsal anterior free margin projecting slightly at the midline. The ventral free margin is emarginated between the projecting mantle locking cartilages. The posterior segment of the mantle tapers gradually to an elongated terminus from which a moderately long tail (TaI = 0.05-0.08) extends.

The fins are large (FLI = 0.48-0.57 and FWI = 0.72-0.81) and muscular with moderately large free lobes present on the convex anterior margin. The lateral margins are sharply rounded and the posterior margins are slightly concave.

The head width is greater than head length (HLI = 0.21-0.25 and HWI = 0.25-0.34) with extremely large eyes (EDI = 0.19-0.21) which occupy about 90% of the lateral surfaces. The nuchal cartilage (Plate 37f) is panduraform with the normal configuration of grooves and ridges. Only one nuchal fold is evident on the posterior lateral surfaces of the head.

The arms are relatively short but muscular and nearly equal in length, arms I = 46% of DML, II = 51% of DML, III = 50% of DML, and arms IV = 48% of DWL. The arm formula is II≥III>IV≥I. The armature of the arms is arranged in four series; the median two series consisting of moderately sized sheathed hooks (Plate 37e) and the lateral two series consisting of large suckers (Plate 37d). The lateral suckers are attached to the short stout trabeculae of a continuous though reduced supporting membrane, as compared with the genus *Gonatus*. In

smaller specimens the median two rows of arm armature consist of small suckers, with those of the lateral series about 1.4 times as large as the corresponding median sucker. The dentition of the suckers of arms I-III is 6-8 teeth. The armature of arms IV consists of four series of suckers, the lateral of which are again about 1.4 times as large as the corresponding median sucker. The dentition of the arm IV suckers is the same as the dentition of arms I-III. Aboral keels are present on arms III and lateral keels are present on arms IV.

The tentacles (Plate 37a) are long (TI = 0.51-0.97) with the sucker bearing area covering between 50-65% of the tentacle length. The armature of the club is arranged in from 5-18 series of varying sized suckers. The dactylus supports a distal circlet of ten small suckers followed proximally by five rows of equal sized suckers which at the junction of the dactylus and manus has increased to six series. The armature of the manus increases from six series on the distal portion to eighteen series intermediately and then decreases to eight series on the proximal portion. The suckers of the manus increase in size from the dorsal and ventral margins medially and both from the base distally and from the junction with the dactylus proximally. The largest suckers of the manus are about three times as large as the smaller lateral suckers.

Along the entire dorsal border of the manus is a fixing apparatus consisting of a series of alternating suckers and fleshy knobs. This series is separated from the rest of the armature by a narrow sucker free strip. A trabeculate supporting membrane is present along the

entire ventral margin of the club and is continuous with a weak membrane present along the entire ventral border of the stalk. The dorsal margin of the stalk also supports a supporting membrane which is continuous with a trabeculate supporting membrane on the dorsal margin of the manus. The dorsal trabeculated supporting membrane terminates on the proximal one-third of the dactylus. A dorsal lateral keel is also present on the dactylus.

Plates 37b and c depict the two types of suckers found on the tentacular club. The suckers of the fixing apparatus display a smooth inner ring while those found on the remainder of the manus have 6-10 long pointed teeth on the distal margin. The first series of polygonal processes on the infundibulum of the manus suckers carries enlarged pegs which in some cases protrude into the mouth of the sucking chamber. The flattened hemicrescent area on the proximal portion of the inner ring is absent and replaced by a single thin flattened process.

The funnel locking cartilage (Plate 37g) is lanceolate with a slightly concave ventral margin and a broad deep central groove. This is opposed by a single cartilaginous ridge on the mantle which flares slightly anterior to posterior. The funnel organ (Plate 37h) consists of a deep U-shaped dorsal pad and two elongate tear-dropped shaped ventral pads. The arms of the dorsal pad widen to present an elongated flattened posterior. A short thick papillae is present at the apex.

Berryteuthis sp.

Larval Stage

The mantle (Plate 38b) is narrow and comparatively thick and muscular (MWI = .31-.37). Anteriorly the mantle is cylindrical in shape while posteriorly the mantle tapers gradually to terminate at the conus of the pen. The ventral anterior margin is notched between the slightly projecting mantle locking cartilages but the dorsal free margin is straight. Large chromatophores cover all surfaces of the mantle. No tail is present.

The fins are small in size (FLI = 0.09-0.13 and FWI = 0.29-0.32) and terminally located with the posterior margin extending beyond the mantle terminus. Each fin is oval in shape with rounded anterior, lateral, and posterior margins. A large chromatophore is present at the dorsal base of each fin.

The head width is greater than head length (HLI = 0.23-0.26 and HWI = 0.33-0.35) and is not withdrawn into the mantle cavity. The eyes are only moderately large (EDI = 0.14-0.16) covering about 60% of the lateral surfaces. The nuchal cartilage is panduraform with only the central groove distinct. Dorsally two chromatophores are located over each eye and an additional chromatophore is located on the midline at the base of arms I. A single chromatophore lies on the ventral surface of each eye with another midway between the eyes.

Arms I-III are stout and muscular and carry four longitudinal series of suckers. The suckers of the two lateral series are about 1.2 times as large as the corresponding median sucker. Arms IV are

weak and covered with four longitudinal series of sucker buds; a barely discernable lateral keel is also present. The arm formula is II>I>III>IV. Each arm carries a single series of large chromatophores on the aboral surface.

The tentacles (Plate 38a) are rod shaped and not much larger than arms II (TI = 0.36-0.41) yet are stouter and more muscular. The flat oral surface is covered by five indistinct rows of suckers. No bare club area is present and the armature is continuous to the distal tip. A series of large chromatophores dot the aboral surface of the tentacle.

The funnel cartilage is lancolate with an indistinct central groove. Opposing the funnel cartilage is a single cartilagenous ridge on the mantle. The funnel organ consists of a shallow U-shaped dorsal pad and two elongate ventral pads. A funnel valve is present.

Genus *Gonatopsis* Sasaki, 1920

Gonatopsis borealis Sasaki, 1923

Adolescent Stage

The mantle of the adolescent stage (Plate 39c) is muscular and anteriorly cylindrical in shape but tappers posteriorly to a pointed terminus (MWI = 0.35-0.46). The anterior free margin is straight dorsally but ventrally emarginated between the projections at the mantle locking cartilages. A short tail (TaI = 0.04-0.06) extends from the terminus of the mantle to the posterior margin of the fin. All mantle surfaces are spotted with relatively large chromatophores.

The fins are large (FLI = 0.21-0.28 and FWI = 0.63-0.74) and muscular. Both the anterior and posterior margins are convex and the lateral margin is sharply rounded. Small free anterior lobes are present. Like the mantle both surfaces of the fins are spotted with relatively large chromatophores.

The head width is greater than head length (HLI = 0.19-0.23 and HWI = 0.28-0.35) and approximately the same width as the mantle opening. The eyes are large (EDI = 0.18-0.20) and cover about 90% of the lateral surfaces of the head. Four nuchal folds are present on the posterior lateral surfaces behind the eyes. A panduraform nuchal cartilage, with the normal configuration of ridges and grooves, is present. The dorsal surface of the head is spotted by relatively large chromatophores with an additional larger chromatophore over each eye. Ventrally a single chromatophore is located on each eye and a larger chromatophore is located on the midline.

The arms are long and muscular (I = 40-48% of DML, II = 44-49% of DML, III = 41-47% of DML and IV = 39-46% of DML) with a formula of II>III≥I≥IV. Large well developed keels are present aborally on arms III and lateraly on arms IV. The armature of all arms consists of four longitudinal series of equal sized suckers. All suckers have 6-8 long blunt teeth on the distal margin of the inner ring. A supporting membrane is present along the lateral series of each arm but is somewhat reduced on arms IV. The aboral surface of all arms is dotted with a single series of large distinct chromatophores. No tentacles are present.

The funnel locking cartilage is lanceolate in shape with a widely flaring deep central groove. This is opposed on the mantle by a single cartilaginous ridge which flares distinctly anterior to postorior. The funnel organ consists of a single large U-shaped dorsal pad and two elongated ventral pads. The arms widen to form distinct shoulders and an elongated flattened lancolike posterior. A long slender papillae originates from a slightly indented apex. The ventral pads are elongate and constrict anterior to posterior. A large funnel valve is present.

Post-larval and Larval Stages

The larval and early post-larval stages are extremely similar in appearance (Plates 30a and 40b). The mantle is widest near the mid-point from which it narrows slightly anteriorly and abruptly posteriorly (MWI = 0.38-0.45). Both the dorsal and ventral free margins of the mantle are straight and no tail is present. All surfaces are spotted with large chromatophores.

The fins are large (FLI = 0.17-0.21 and FWI = 0.48-0.52) and relatively muscular. Rounded lateral and convex anterior and posterior margins impart an oval appearance to the fins. The chromatophores on the fins consists of a pair at the dorsal point of attachment with the mantle.

The head is large and of greater length than width (HLI = 0.18-0.33 and HWI = 0.33-0.42). An ovoid shape is imparted to the head by large bulbous eyes (EDI = 0.15-0.20) which cover about 85% of the lateral surfaces. The head of the earlier phases is almost completely withdrawn

into the mantle cavity. The nuchal cartilage is panduraform in shape with only the central ridge and groove distinct. The dorsal surface of the head carries a single large chromatophore over each eye and an additional one at the juncture of arms I. The ventral surface exhibits the same chromatophore arrangement as the dorsal surface, one on each eye and an additional one medially at the base of arms IV.

The arms are short, stout, and muscular (I = 29-32% of DML, II = 34-39% of DML, III = 27-34% of DML, and IV = 21-26% of DML). Large aboral keels are present on arms III even on the smallest specimens whereas the latest keels on arms IV are indistinct. The armature of all specimens examined consisted of four longitudinal series of suckers. The distal tips of arms I-III and the distal one-third of arms IV are sucker buds. A supporting membrane is not evident although the lateral series are supported by small trabeculae.

One specimen of DML = 9.23 mm had a single thin rod-like tentacle present. The distal tip of this tentacle was degenerated but carried seven suckers which were functional in appearance. The oral surface of the tentacles, when present, support from 5-6 longitudinal series of small suckers which diminish rapidly, covering only the distal two-thirds of the tentacle. At the base the armature terminates with three large suckers, 2-2.5 times the size of the other armature. The tentacles of the larval stage exhibit the same armature arrangement as the post-larval stage but without the degenerated tip.

The funnel locking cartilage and funnel organ are similar to the adolescent stage only proportionally smaller. The mantle segment of

the locking cartilage flares distinctly anterior to posterior. A funnel valve is present.

Developmental variations

By evaluating changes in the relative proportions of arms, tentacles, head, fins and mantle width in relation to mantle length some systematic comparisons can be made. A summary of the relative growth of various body parts for five species of squid from the genus *Gonatus* is given in Table 1. Though different rates were evident the relationships observed tended to either increase or decrease throughout growth. In only one case was a reversal of growth tendency observed; the relative proportion of the tentacle length of *Gonatus madokai* decreased between the larval and post-larval stages and increased between the post-larval and adolescent stages. This reversal resulted in no net change in the relative proportion of the tentacle between the larval and adolescent stages.

Generally speaking, the body tends to become narrower and more streamlined; this trend is evident by the decrease in relative mantle and head widths. Corresponding with this change is the development of a relatively larger fin. A concurrent increase in both fin length and fin width was observed in all species except *Gonatus* type A in which the relative proportion of the fins remained constant. The muscular condition of the mantle and fins also exhibits a gradual change with the relative changes in body form. The mantle and fins of the larval stage are generally weak and flacid but by the adolescent stage are

Table 1. Summary of the relative growth of various body parts for species from the genus *Gonatus*. The parts either decrease (D), increase (I), or remain constant (C) in relation to the DML during growth.

Species	*G. onyx*	*G. madokai*	*G. tinro*	*G.* sp.	*G.* type A
Body part					
MW	D	D	D	D	D
FL	I	I	I	I	C
FW	I	I	I	I	C
HL	C	I	C	D	C
HW	D	D	D	D	D
ED	I	D	I	I	D
T	D	C	I	D	D
I	I	I	I	I	I
II	I	I	I	I	C
III	I	I	I	I	C
IV	I	I	I	I	I

strong and well formed. This gradual change is evident in all species of the genus *Gonatus* with the exception of *Gonatus madokai* in which the musclature remains relatively weak throughout development.

An overall increase in relative arm lengths was also evident and undoubtedly corresponds with the development of suckers and changes in feeding habits. It is interesting to note that in only one species, *Gonatus tinro*, did a corresponding increase in relative tentacle length take place. *Gonatus tinro* is the only member of this genus which does not develop a large central hook on its tentacular clubs and thus may require relatively longer tentacles for capturing more active and larger prey. A corresponding decrease in relative tentacle size was evident in three of the five species evaluated while in one species, *Gonatus madokai*, the relative size at first decreased and then increased. A variety of relative growth was exhibited for the eye diameter and head length in those species evaluated.

Throughout the family the general chromatophore pattern changes from a few large scattered chromatophores to numerous small densely packed chromatophores. In the juvenile stages the ventral surfaces of the mantle and fins always have fewer chromatophores than the dorsal and lateral surfaces. The immature stages also have at least one, but usually two or three, chromatophores present on the dorsal surface of each eye and at least one additional chromatophore present on the dorsal midline of the head. The ventral surface of the head exhibits a similar pattern, however, only one small chromatophore is usually present on the ventral surface of each eye.

The tentacles and arms always support a single series of large chromatophore on the aboral surfaces. Additionally, on the arms a small chromatophore was usually evident at the anterior base of each trabeculae.

Figure 6 illustrates the changes in arm armature which takes place during growth. Although different timing is evident this development takes place in a systematic progression in all species. The arm armature is initially present as four longitudinal series of sucker buds with occasionally one or two small suckers present at the base of the largest arm (this appears to always be the case for *Gonatus onyx*). With development these buds metamorphose into suckers from the base of the arm distally. No further change occurs in the armature until the sucker buds are fully converted into suckers on all but the tip of the arm, growth in the arm occurs at the distal tip and therefore a few sucker buds are always present throughout development.

The final phase in arm armature development is the conversion of the median two series into hooks. This conversion initiates in the largest suckers, which are usually found in the midregion of the arms, and proceeds both distally and proximally from this point. The distal most median suckers are never converted into hooks even in the largest specimens.

In two-thirds of the species examined sucker development begins to take place between 8-9 mm (*Gonatus madokai, G. tinro, G. onyx* and *G.* sp.) while in *Gonatus berryi* sucker development takes place prior to 6 mm and in *Gonatus* type A after 12 mm. Once sucker and hook development is

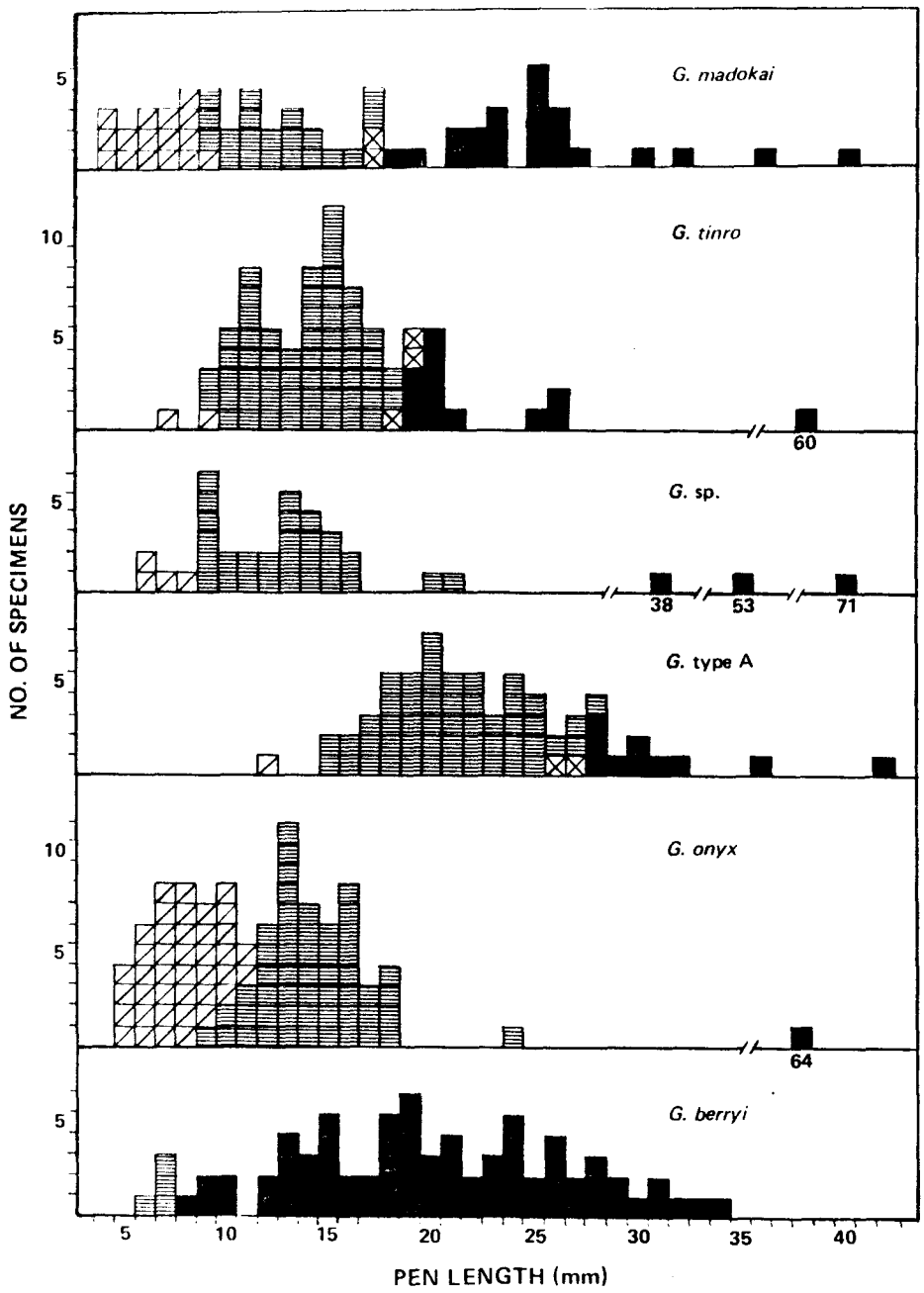


Figure 6. Arm armature development for species of *Gonatus*. The slashed squares indicate pre-sucker development, striped squares indicate suckers present, X's indicate intermediate development (first hint of hook development) and solid squares indicate hooks present. Data for *G. berryi* from Young (1972) and present study.

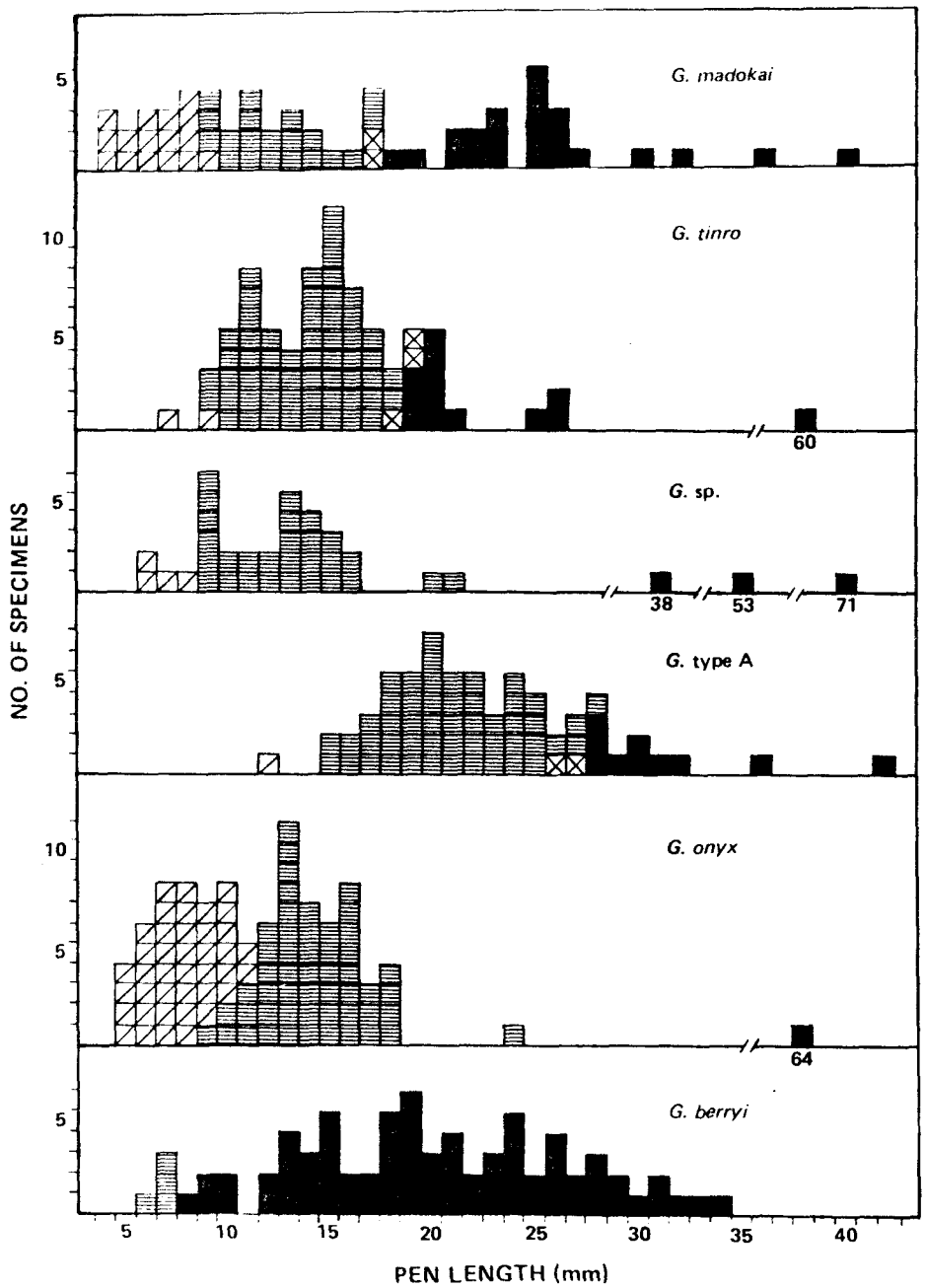


Figure 6. Arm armature development for species of *Gonatus*. The slashed squares indicate pre-sucker development, striped squares indicate suckers present, X's indicate intermediate development (first hint of hook development) and solid squares indicate hooks present. Data for *G. berryi* from Young (1972) and present study.

initiated it progresses rapidly. This is apparent from the relatively few intermediate conditions found. Kristensen (1977) noted a similar rapid development of the club armature of *Gonatus fabricii*.

The sequential maturation of the tentacle armature is shown in Figures 7-11. The larval stage of each species has a small sucker free club at the distal tip of the tentacle. With an increase in body size sucker buds appear simultaneously on all surfaces of the club which, as development progresses, become arranged in patterns similar to the adult.

Sucker development proceeds from the tip of the dactylus, excluding the circlet, proximally. Suckers do not usually appear on the dorsal- or ventral-marginal zones until sucker development on the dactylus is nearly complete; at which time suckers develop simultaneously on both zones. This development is followed by the maturation of the proximal and distal armature of the median zone. The large central hook of the median zone starts development concurrently with the maturation of the dactylus. Finally the armature on the dorsal and ventral margins of the stalk develop.

A comparison between species of the body size during development of the club armature is also possible from Figures 7-11. The development of each zone takes place at approximately the same size in *Gonatus onyx* and *Gonatus* sp. while development proceeds later in *Gonatus madokai* and last in *Gonatus* type A. The small amount of data available indicate that *Gonatus berryi* starts armature development somewhat later than *Gonatus onyx* and *Gonatus* sp. but prior to *Gonatus madokai*.

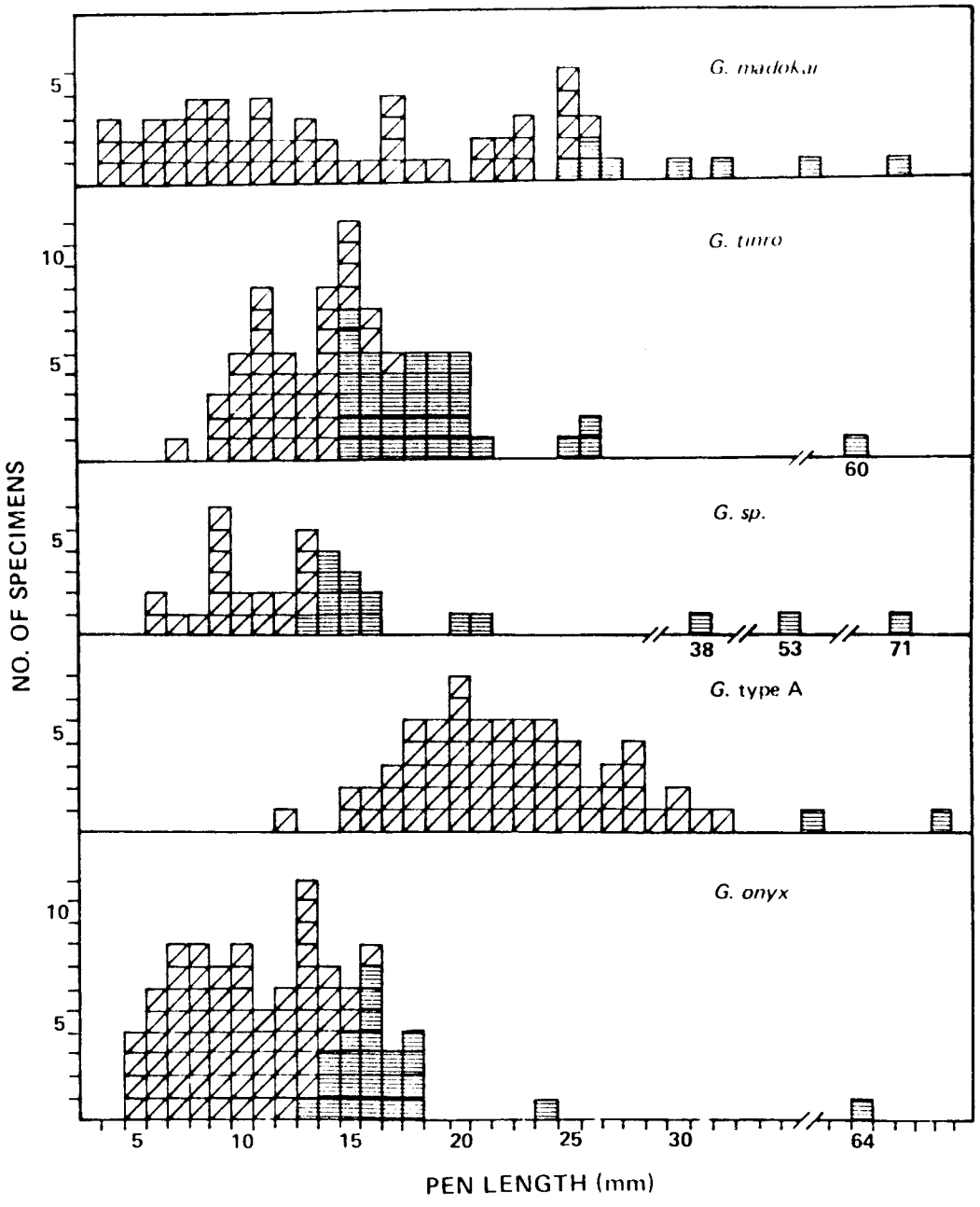


Figure 7. Dactylus armature development for species of *Gonatus*. The slashed squares indicate pre-sucker development, striped squares indicate suckers present, X's indicate intermediate development (first hint of hook development) and solid squares indicate hooks present.

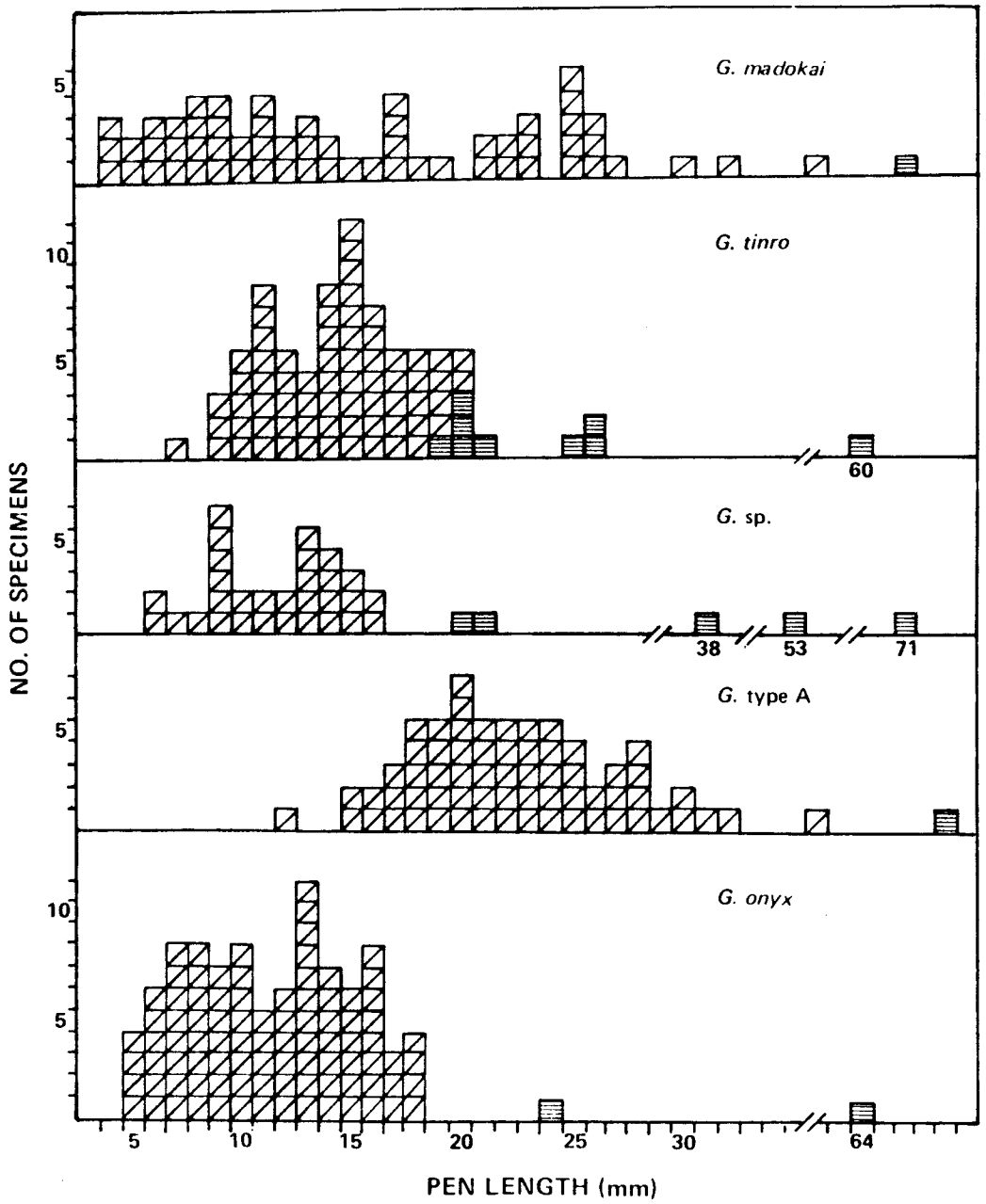


Figure 8. Dorsal-marginal zone armature development for species of *Gonatus*. The slashed squares indicate pre-sucker development, striped squares indicate suckers present, X's indicate intermediate development (first hint of hook development) and solid squares indicate hooks present.

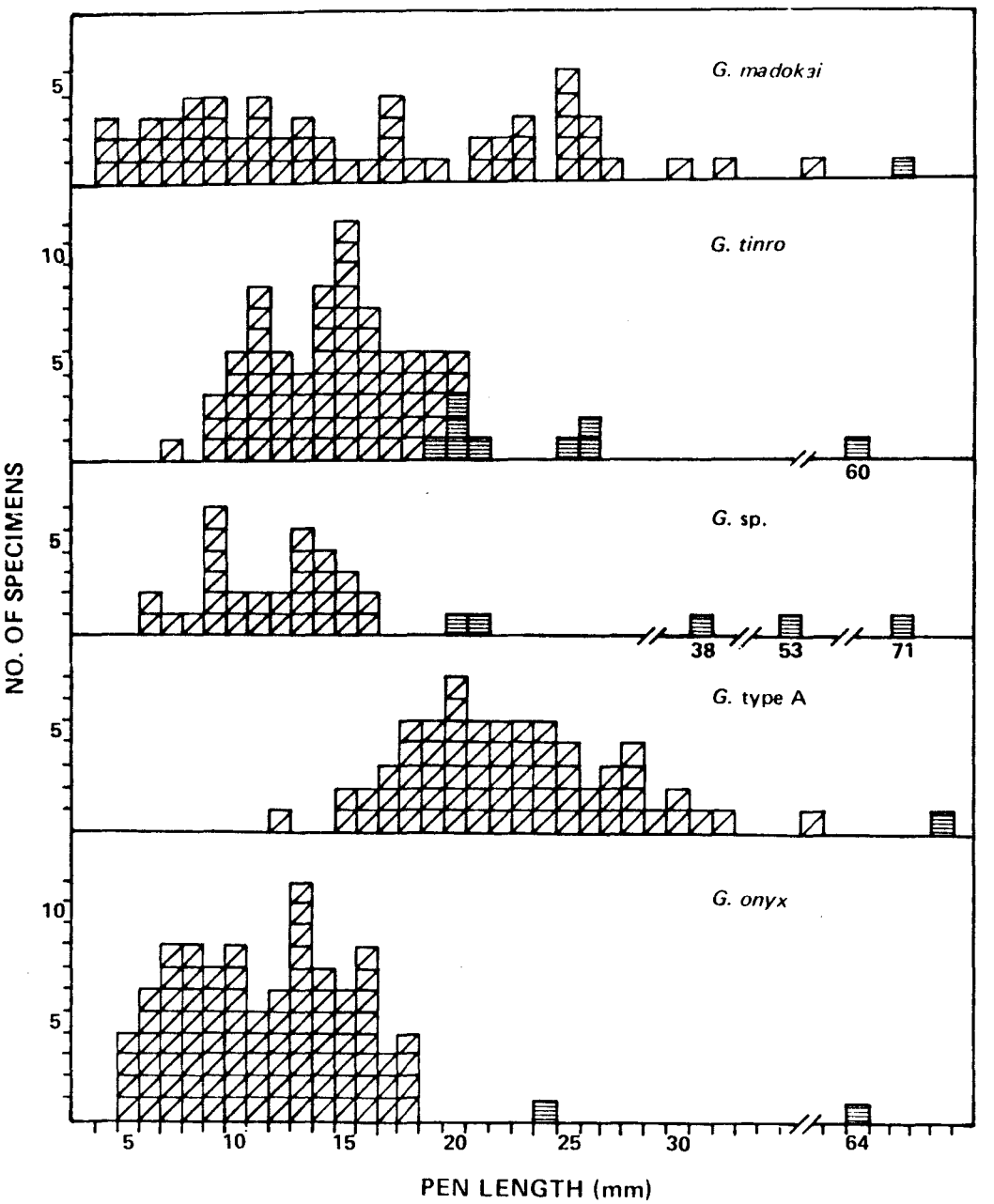


Figure 9. Ventral-marginal zone armature development for species of *Gonatus*. The slashed squares indicate pre-sucker development, striped squares indicate suckers present, X's indicate intermediate development (first hint of hook development) and solid squares indicate hooks present.

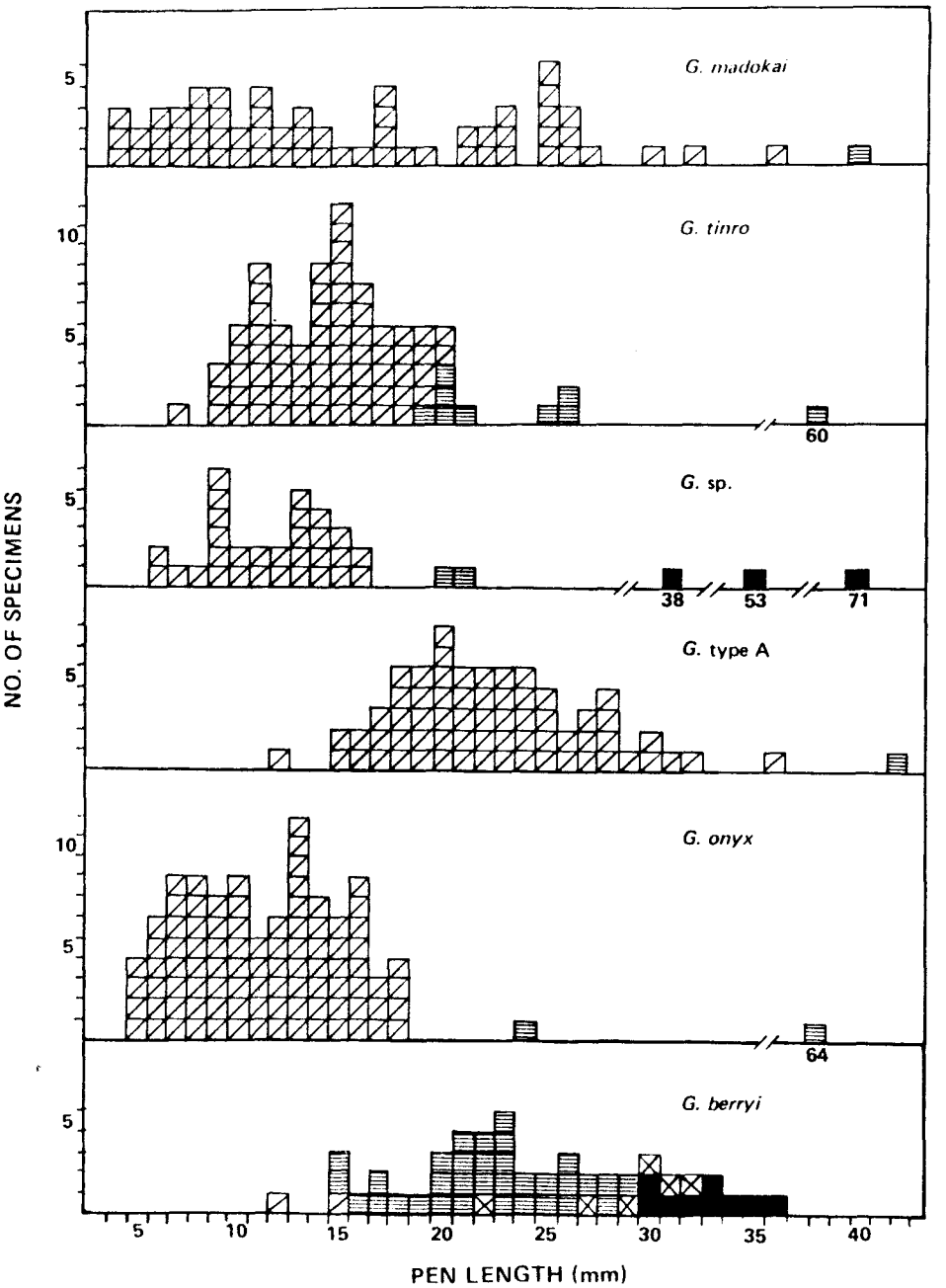


Figure 10. Median zone proximal hook development for species of *Gonatus*. The slashed squares indicate pre-sucker development, striped squares indicate suckers present, X's indicate intermediate development (first hint of hook development) and solid squares indicate hooks present. Data for *G. berryi* from Young (1972) and present study.

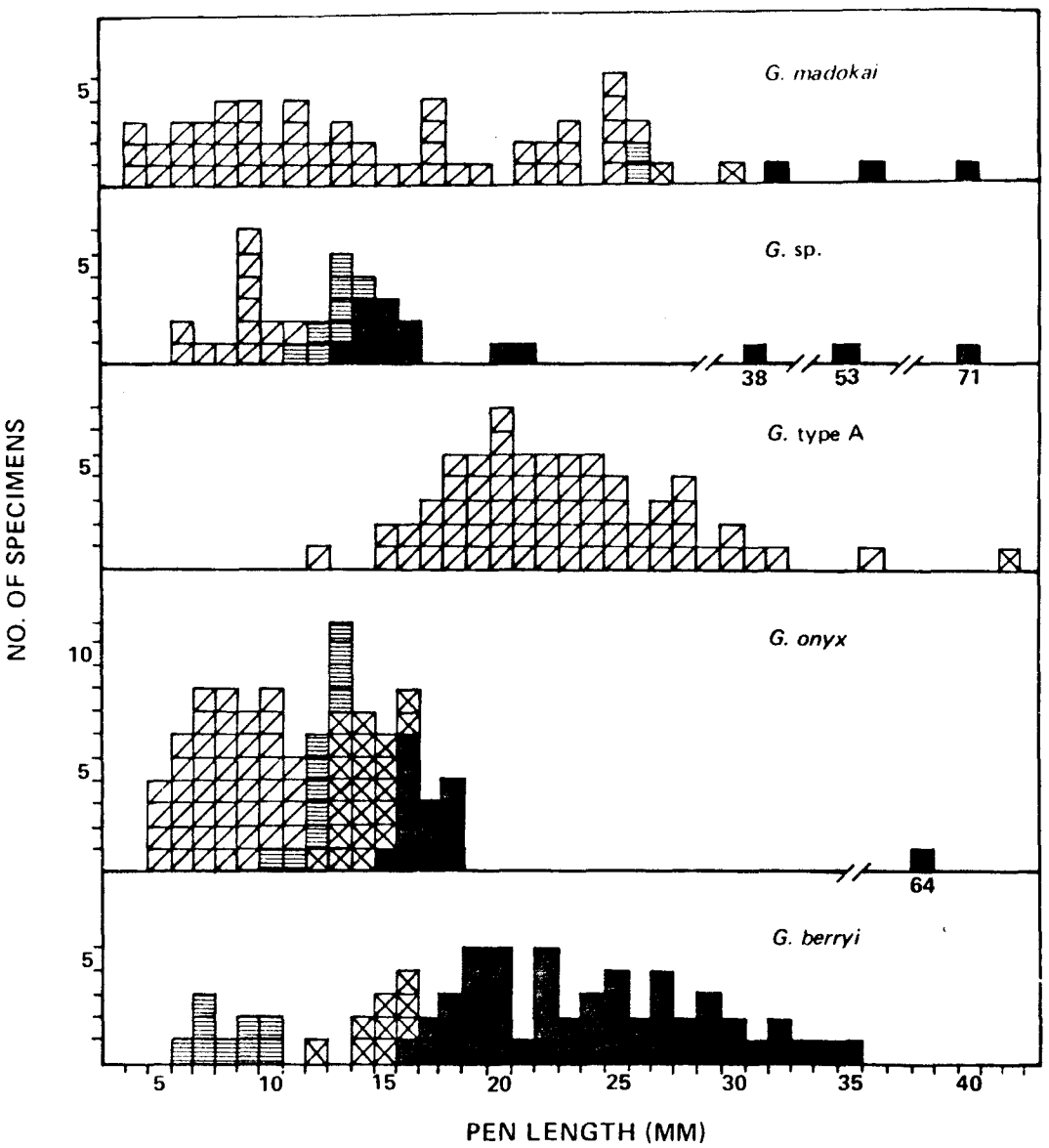


Figure 11. Median zone central hook development for species of *Gonatus*. The slashed squares indicate pre-sucker development, striped squares indicate suckers present, X's indicate intermediate development (first hint of hook development) and solid squares indicate hooks present. Data for *G. berryi* from Young (1972) and present study.

CHAPTER 4

DISCUSSION

Systematic Comparison

A total of 1,214 specimens of *Gonatus onyx*, ranging in size from 5.21 to 66.63 mm DML, were collected between 1977 and 1979. The systematic characteristics of the adult and late adolescent specimens of this species coincide closely with Young's (1972) description. The relative size and armature arrangement of the arms and tentacles are in close agreement; however, the development of the club armature is slightly earlier than that reported by Young (1972). He reported hook development on the arms at between 26-28 mm PL and on the tentacular club at between 17-24 mm PL. The data from this study indicate hook development on the club takes place between 12-16 mm PL. Arm hook development was not evident from these data. Young (1972) also reported the presence of gelatinous aboral keels on arms I-III which were not discernable on these specimens. Okutani (1966, Plate I, Figures 3 and 3a) briefly described a specimen of *Gonatus fabricii* that appears to be an adolescent *Gonatus onyx*; a similar specimen is described by Okutani and McGowan (1969, Figures a and b).

Earlier developmental stages of this species coincide with descriptions of *Gonatus fabricii* by Okutani (1966, Plate I, Figure 4; and 1968, Plate III, Figure 6) and Okutani and McGowan (1969, Figures 10e, f and g) and closely resemble the description of *Gonatus* type C given by Kubodera (1978, Plate XVIII, Figures a-f). The specimens from this

study also include the larval stage of this species which has not been previously described.

A total of 514 specimens of *Gonatus madokai*, size range 4.32-42.28 mm DML, were taken from the study area. The adolescent, post-larval, and larval stages of development all agreed closely with the descriptions given by Kubodera and Okutani (1977) and Kubodera (1978) with a slight difference in arm formula, the only discrepancy. The preceding descriptions give an arm formula of III>II>I>IV whereas the data compiled from this study indicate formulae of II=III>I>IV in the adolescent and post-larval stages and II≥III>I>IV in the larval stage. The specimens from the study area also closely resemble those of Sasaki (1929, Plate XXII, Figure 10) *Gonatus fabricii* as well as those described by Okutani (1966, Plate III, Figure 2) as post-larval *Gonatus* type γ and larval *Gonatus fabricii* (Plate I, Figure 5).

A total of 181 specimens of *Gonatus tinro*, ranging in size from 7.90 to 63.89 mm DML, were available for study. The adults and late adolescent stage specimens are the same, with variations in the arm formula, as those described by Fields and Gauley (1971) and Nesis (1972). Fields and Gauley reported an arm formula of II=III>IV>I for the adult and III>II=IV>I for the adolescent, while Nesis reports a formula of II=III>I≥IV throughout development. The specimens taken from the southeastern Bering Sea exhibited an arm formula of II≥III≥I≥IV for the adult, II≥III>I≥IV for the adolescent and II≥III>I>IV for the post-larval and larval stages.

Kubodera (1978) described young stages of *Berryteuthis magister* (Plate XII, Figures a-e) which closely resemble the juvenile stage of *Gonatus tinro* depicted by Nesis (1972, Figures 13-15). Specimens from the study area could not be separated by external characteristics on the basis of either Nesis' (1972) or Kubodera's (1978) descriptions. An examination of the radular of 32 specimens has shown that each carries only five longitudinal rows of teeth - characteristic of the genus *Gonatus* (Plate 41). A comparison of these with a known post-larval specimen of *Berryteuthis anonychus* (Plate 42) indicated that the specimens in question belonged to *Gonatus tinro*. A comparison of the radulae of Kubodera's (1978) specimens and those taken from the southeastern Bering Sea was not made and therefore existing differences were not determined.

A total of 171 specimens categorized as *Gonatus* type A and ranging in size from 12.90 to 42.13 mm DML were taken from the study area. These specimens differed only in the arm formula for the adolescent and post-larval *Gonatus* type A reported by Kubodera (1978). He reported an arm formula of II>III>I>IV throughout development; however, the specimens in this collection show a formula of II>III>I>IV for the adolescent stage and II=III>I>IV for earlier development. The data from this study also indicate that the lateral suckers of the arms are larger than the median suckers; whereas Kubodera (1978) did not indicate a difference in sucker size. The specimens reported here also include the larval stage which has not previously been described.

This type superficially resembles *Gonatus californiensis* described by Young (1972); however, several differences exist which separate the two. In *Gonatus* type A the lateral suckers of arms IV are larger than the corresponding median sucker; whereas Young (1972) reported for *Gonatus californiensis* that the median row suckers of arms IV were the largest. The armature of the dorsal-marginal zone also differs; five rows for *Gonatus* type A versus 2-3 rows for *Gonatus californiensis*. Another difference is evident in the fact that the large median hook of *Gonatus californiensis* develops at around 17 mm PL whereas the central hook of *Gonatus* type A develops around 42 mm PL.

This type more closely resembles the brief description of *Gonatus kamtschatica* given by Middendorf (1849). His description indicates the presence of five longitudinal series of large suckers on the ventral margin of the club which are continuous with a series of papillae on the margin of the stalk; "5 grössen Saugnäpfe stehen hintereinander auf dem Rande der Basis des Kolbenendes, und als Fortsetzung dieser Reihe lässt sich eine dichte Reihenlinie sehr kleiner Papillchen den ganzer Stiel des Fang-Armes entlang verfolgen" (Middendorff, 1849, p. 187). The presence of papillae on the stalk of a relatively large specimen indicates a late development which coincides with *Gonatus* type A. Consequently *Gonatus* type A may conceivably be a juvenile *Gonatus kamtschatica*.

Seven specimens of *Gonatus berryi* were available from the southeastern Bering Sea; four from 1978 and three museum specimens. The samples ranged in size from 12.12 to 29.90 mm DML and all specimens

were in either the adolescent or post-larval stage of development. The larger specimens were identical in characteristics to the adult and brief larval descriptions given by Young (1972). Kubodera (1978) also described an adolescent member of this genus (*Gonatus* type D, Plate XIX) from the southcentral Bering Sea.

A total of 160 specimens of *Gonatus* sp., ranging in size from 6.99 to 79.56 mm DML, were taken from the study area. Three specimens were adult and eleven were late adolescent stages with the remainder either early adolescent, post-larval, or larval stages. The adult and late adolescent stages of this species superficially resembles *Gonatus berryi* in the general shape and relative size and condition of the mantle, arms, and fins. Significant differences are apparent on the tentacles and in development to separate the two (specimens examined included several *Gonatus berryi* on loan from the Smithsonian Institution and Dr. Young, University of Hawaii).

The tentacular clubs of *Gonatus* sp. are relatively smaller, 21-23% versus 30-37% of the DML, than those of *Gonatus berryi*, and the armature of the manus exhibits several differences. The ventral-marginal zone of *Gonatus berryi* bears two lateral series of large suckers with a single series of minute suckers medially versus three lateral series of large suckers and a single series of minute median suckers. Both species bear the remnants of an additional minute series. The dorsal-marginal zone of *Gonatus* sp. also bears two additional series of suckers, four versus two in *Gonatus berryi*.

The median zone of the manus also differs considerably. Young (1972, p. 47) referring to *Gonatus berryi* states, "the median zone contains a large central hook followed distally by a small hook and preceeded proximally by a single series of suckers and hooks. One or two suckers always lie nearest to the large hook and are followed by 2-4 hooks; the largest hook is never the closest one to the large central hook". *Gonatus* sp. exhibits the same arrangement of a large central hook and a smaller distal hook; however, the proximal series differs. In this case there are no suckers present and the entire series consists of hooks.

The stalk armature of *Gonatus* sp. also differs slightly from *Gonatus berryi*. The sucker series along the ventral margin of the stalk of *Gonatus berryi* is continuous throughout its length. On the stalk of *Gonatus* sp. this series is present only on the distal one-sixth.

Differences in dentition are also evident. In *Gonatus berryi* the suckers of the dactylus have 6-8 short relatively blunt teeth; however, in *Gonatus* sp. the larger dactylus suckers have 8-10 long slender pointed teeth and the smaller suckers have 6-8 shorter blunter teeth. Young (1972) also reported 8-9 teeth on the suckers of the ventral-marginal zone for *Gonatus berryi* but the suckers from this zone of *Gonatus* sp. have only 6-8 teeth.

A major difference in development between the two species is illustrated in Figure 6. The metaporphoses of the median arm hooks on *Gonatus berryi* occurs extremely early in development (about 8 mm PL).

Specimens of *Gonatus* sp., however, had not developed hooks prior to 21 mm PL but hooks were present at 38 mm PL. The presence of several developmental stages of both species in the southern Bering Sea and the significant differences in armature arrangement and development strongly indicate that *Gonatus* sp. is not a variation of *Gonatus berryi*.

Due to the limited number of samples of mature *Berryteuthis anonychus* and *Berryteuthis magister* and the lack of intermediate sizes of both species only a brief discussion of this genus can be given. The adult stages of *Berryteuthis magister* and the adolescent stages of *Berryteuthis anonychus* coincide with the descriptions given by Berry (1913), Kubodera (1978), Naef (1923), Pearcy and Voss (1963), and Sasaki (1929). The larval stage designated *Berryteuthis* sp. also closely resembles the description given by Kubodera (1978) for *Berryteuthis anonychus* larvae; however, this description was partially reliant upon the designation of other larval types as *Berryteuthis magister*. Samples resembling his descriptions of juvenile *Berryteuthis magister* were found to be *Gonatus tinro*; consequently it was felt that insufficient evidence was available to identify these specimens to the species level.

Only 28 specimens of *Gonatopsis borealis* were available for analysis, the adolescent stage of which coincides with the descriptions given for this species by Sasaki (1923) and Young (1972). In his brief description of the larvae Young (1972, p. 60) indicated that, "near the base of the tentacle lie 1-3 enlarged suckers". This characteristic was also evident in specimens from the Bering Sea and consequently

specimens could be identified to the larvae state even though a limited number were available.

Systematic Separation

The adult and adolescent stages of *Gonatus onyx* and *Gonatus tinro* and the adult stage of *Gonatus pyros* have unique features which easily separate them from other members of the genus. The remaining four members; *Gonatus madokai*, *Gonatus berryi*, *Gonatus* sp., and *Gonatus* type A; are not as easily separated and can only be differentiated by the sucker and hook patterns on the tentacular club.

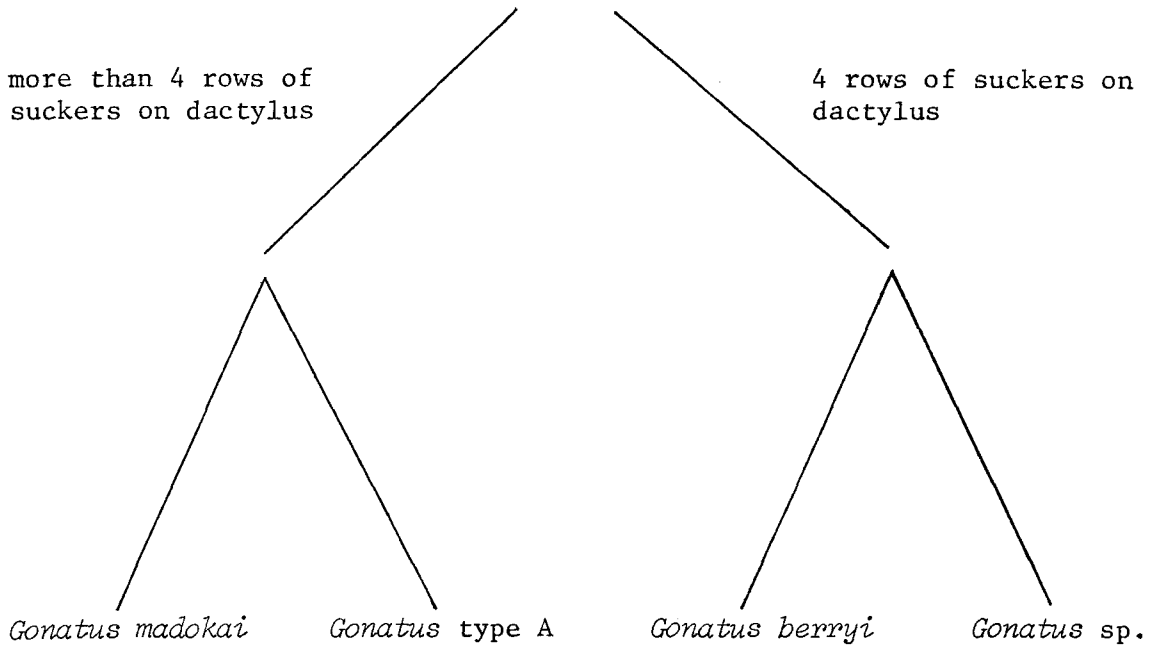
Gonatus tinro and *Gonatus pyros* are both unique within the genus. *Gonatus tinro* possess a club which does not bear a large central hook and *Gonatus pyros* is the only member of this genus which possesses photophores. *Gonatus onyx* has the complex tentacular club typical of other members of the genus; however, the median zone carries only a single large central hook. The median zone of this species lacks the smaller distal hook and the small proximal hooks that are present in all other species except *Gonatus tinro*.

The adult stage and the late adolescent phase of the remaining four members of this genus are separable by the arrangement of suckers and hooks on the tentacular club (Figure 12). *Gonatus madokai* and *Gonatus* type A can be separated from *Gonatus berryi* and *Gonatus* sp. by the dactylus sucker patterns. The latter two have four rows of suckers throughout the entire length of the dactylus whereas the former two

Species possessing unique characteristics.

Gonatus pyros - photophores on eyes
Gonatus tinro - no hooks on club
Gonatus onyx - only one hook on club

Species separable using tentacular club characteristics.



	Gonatus madokai	*Gonatus* type A	*Gonatus berryi*	*Gonatus* sp.
*v-m.	6 rows	5 rows	3 rows	4 rows
d-m	6 rows	4 rows	2 rows	4 rows
dact.	8 rows	10 rows	--	--
med.	--	--	suckers/hooks	hooks only

* v-m: ventral-marginal zone, d-m: dorsal-marginal zone, dact.: dactylys, med.: median zone.

Figure 12. Systematic characteristics of the adult and late adolescent stages of the genus *Gonatus*.

have an increasing number of longitudinal rows from the distal portion toward the base.

Gonatus madokai is separable from *Gonatus* type A by a close examination of the other sucker bearing areas of the club. The median zone of both members possesses two distal hooks followed by a proximal series of suckers. However, the ventral-marginal zone of *Gonatus madokai* bears six longitudinal rows at its widest point whereas *Gonatus* type A has only four. There are six rows of suckers decreasing distally to three on the dorsal-marginal zone of *Gonatus madokai* and five decreasing to four on *Gonatus* type A. The dactylus of the two also show slight differences; *Gonatus madokai* has eight rows at the base while *Gonatus* type A possesses ten.

The armature of the manus can also be used to separate the remaining two species. The ventral-marginal zone of *Gonatus berryi* carries two lateral series of large suckers and one median series of minute suckers. *Gonatus* sp. on the other hand has three lateral rows of large suckers and one median row of minute suckers on this area. The armature of the dorsal-marginal zone also differs between the species; where *Gonatus berryi* has two series throughout this region *Gonatus* sp. has four rows which decrease distally to two rows. The median zone likewise varies, in *Gonatus* sp. a single series of hooks is present proximal to the large central hook, whereas both suckers and hooks are present on *Gonatus berryi*.

The early adolescent phase and the post-larval and larval stages of the genus *Gonatus* are more difficult to separate with any assurance

(Figure 13). *Gonatus madokai* and *Gonatus* type A are the most easily separable. Throughout the early developmental stages *Gonatus madokai* exhibits a constricted and elongated brachial crown which is easily distinguishable. *Gonatus* type A possesses a unique sucker pattern on the tentacular stalk consisting of a distal group of four regimented series followed proximally by four staggered series.

Of the remaining four species the stalk armature of *Gonatus onyx* and *Gonatus tinro* consists of six staggered longitudinal series while the stalk armature of *Gonatus berryi* and *Gonatus* sp. consist of five staggered longitudinal series. Some difficulty may be experienced in separating *Gonatus onyx* and *Gonatus tinro* because the most obvious characteristic is the separated epidermis which is present on *Gonatus onyx*. This epidermis is easily torn off and thus can lead to confusion especially in the earlier stages. *Gonatus onyx*, however, develops a differentiated club which possesses a central hook bud early in the post-larval stage, whereas the developing tentacle of *Gonatus tinro* is rod shaped and the club bears only densely packed sucker buds.

The tentacular stalk of *Gonatus berryi* and *Gonatus* sp. both carry five staggered longitudinal series of suckers. This arrangement causes difficulties in the separation of the larval and post-larval stages. This difficulty is circumvented by a comparison of the time of development of the large central hook and the arm hooks. Figure 6 illustrates a major developmental difference between the two species. The size of the organism at the development of the central hook is relatively the same but the size at which the arm hooks develop is considerably

Species possessing unique characteristics.

Gonatus madokai - constricted and elongated brachial crown
Gonatus type A - 4/4 sucker pattern on tentacular stalk

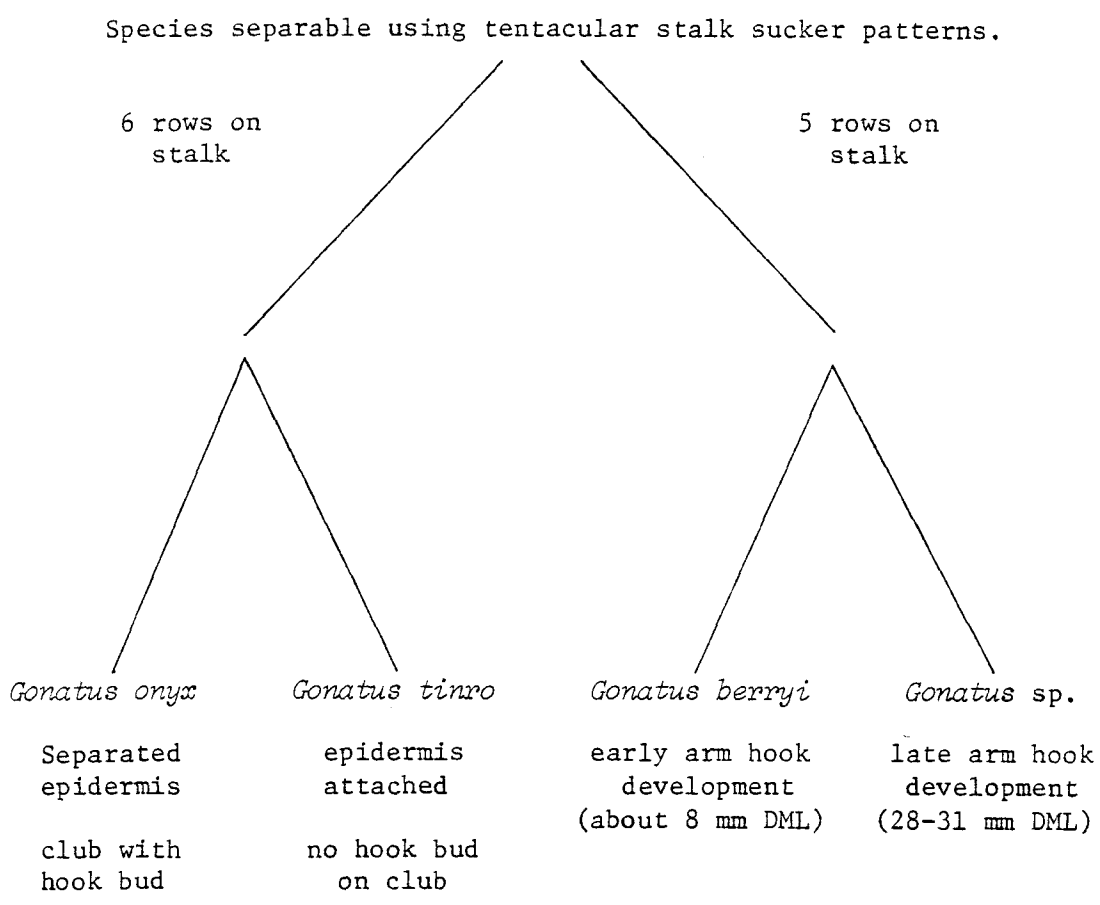


Figure 13. Systematic characteristics of the early adolescent, post-larval, and larval stages of the genus *Gonatus*.

different. These hooks develop at about 8 mm pen length in *Gonatus berryi* and somewhere between 21 and 38 mm pen length in *Gonatus* sp.

The two members of the genus *Berryteuthis* are easily separable in the adult stage. *Berryteuthis anonychus* possesses a club which bears equal sized suckers throughout; *Berryteuthis magister* on the other hand has a tentacular club with suckers which increase in size toward the center of the manus. *Gonatus tinro* resembles members of this genus in the fact that the club carries numerous rows of suckers and no central hook. However, this species is separable from members of the genus *Berryteuthis* by the fact that the club possesses a locking zone typical of the genus *Gonatus*; whereas the fixing apparatus of the genus *Berryteuthis* is present along the entire dorsal border of the manus and lacks corresponding grooves and ridges.

The lack of specimens for some species make a complete and definitive analysis of this family impossible. Adult stages of *Gonatus madokai* and *Gonatus* type A and the larval, post-larval, and adolescent stages of *Gonatus pyros* are needed to complete the systematic characterization of the genus *Gonatus*. A complete range of developmental stages are needed for both members of the genus *Berryteuthis* and for all species of the genus *Gonatopsis* to complete the systematic analysis of this family.

SUMMARY

1. Ten species of pelagic cephalopods from the family Gonatidae are described.

2. Adult, adolescent, post-larval and larval stages are described for *Gonatus onyx*, *Gonatus tinro* and *Gonatus* sp.

3. Juvenile stages for five species; *Gonatus madokai*, *Gonatus berryi*, *Gonatus* type A, and *Berryteuthis anonychus*, are described.

4. Descriptions are given for the adult stage of *Gonatus pyros* and *Berryteuthis magister*.

5. The larval stage of a member of the genus *Berryteuthis* is described.

6. A probable new species of the genus *Gonatus* is identified.

7. The presentation of a complete growth series of *Gonatus tinro* firmly establishes the authenticity of this species.

8. Two closely allied species, *Gonatus* sp. and *Gonatus berryi*, are compared and contrasted.

9. Juvenile stages of what appear to be *Gonatus kamtschatica* (herein designated as *Gonatus* type A) are presented.

10. A systematic analysis of growth and development within the genus *Gonatus* is given.

11. A systematic analysis of the taxonomic characteristics of all ten species is also presented.

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APPENDIX A

DISTRIBUTION AND ABUNDANCE OF LARVAL CEPHALOPODS

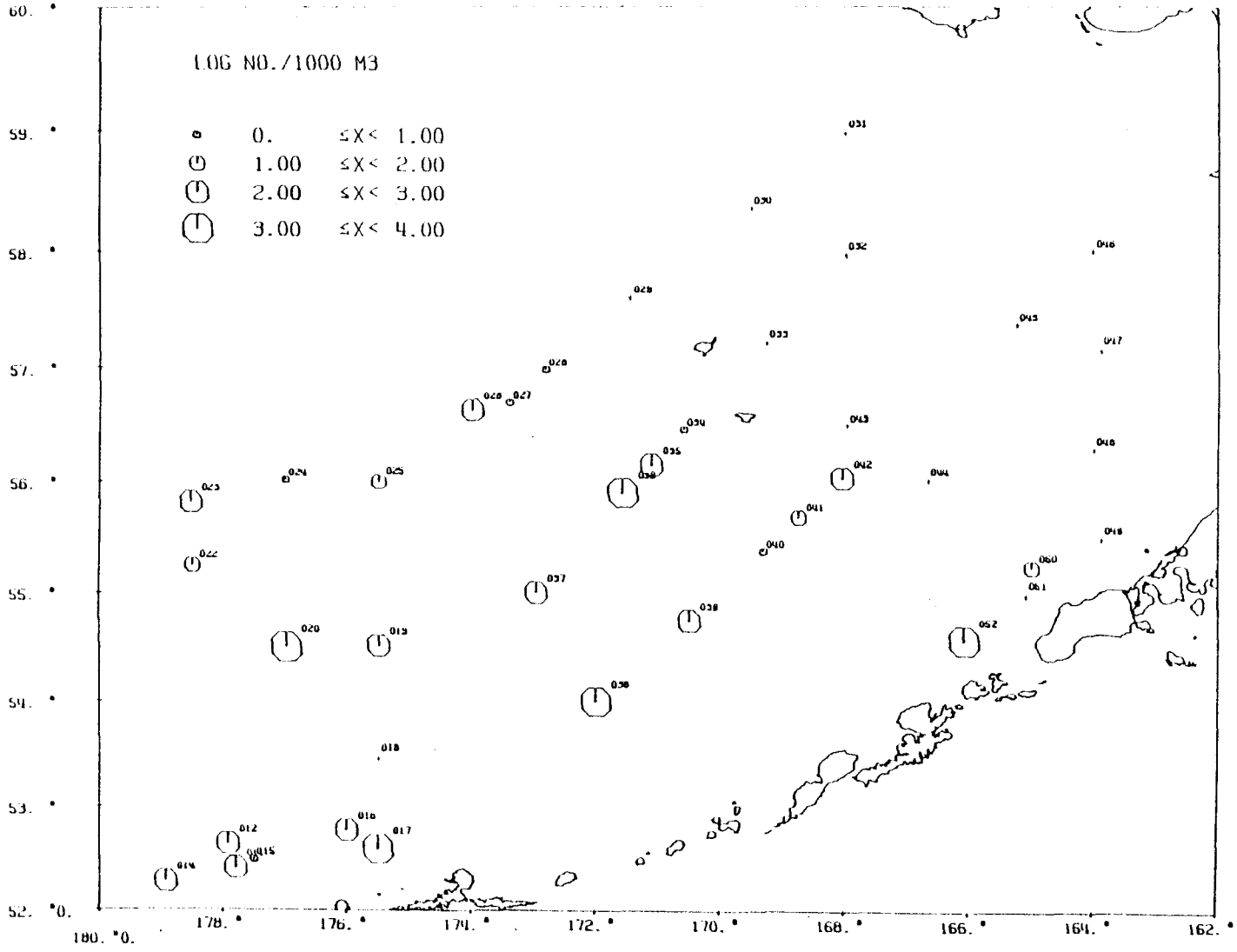

Figure A-1. June, 1977 cephalopod distribution.

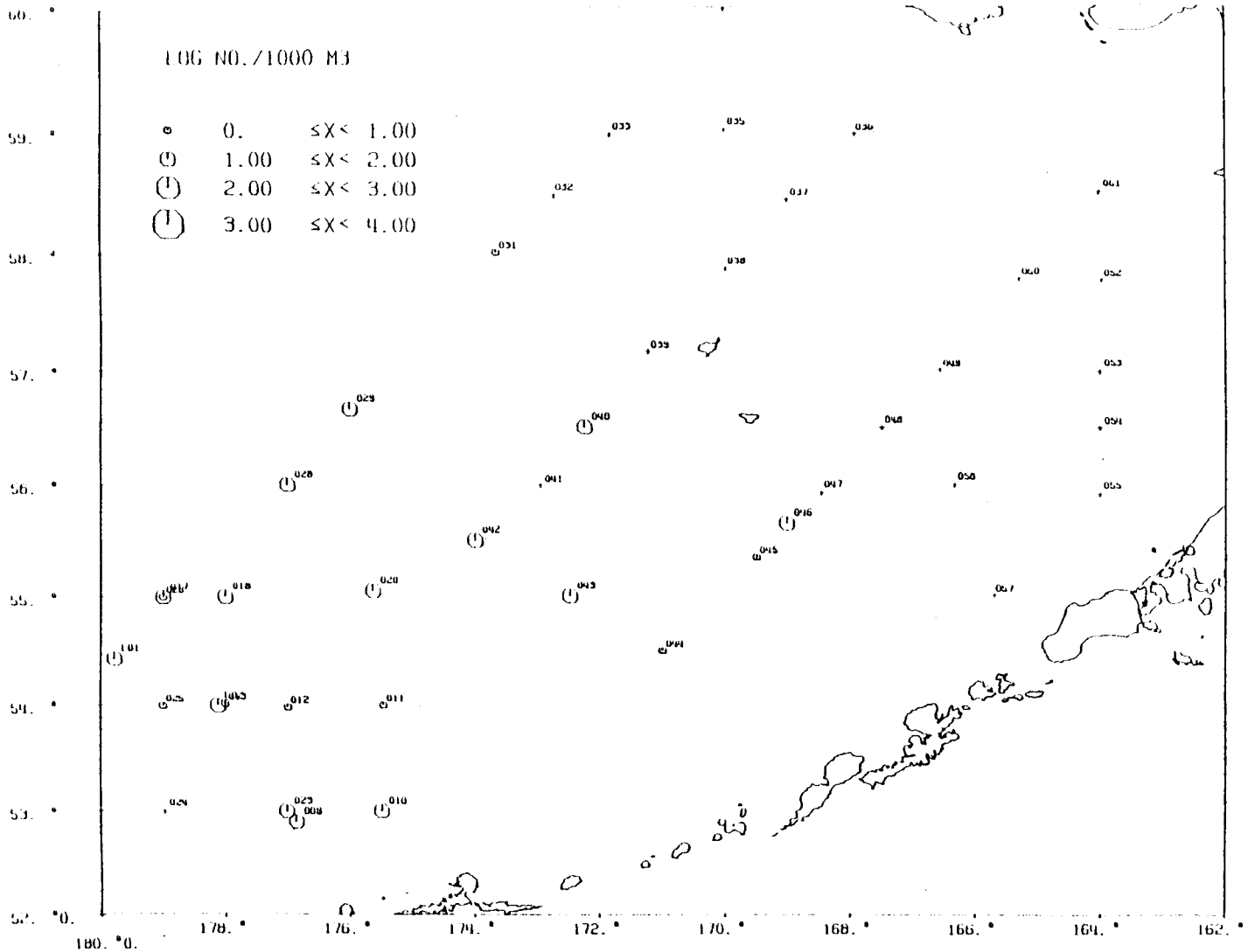

Figure A-2. June, 1978 cephalopod distribution.

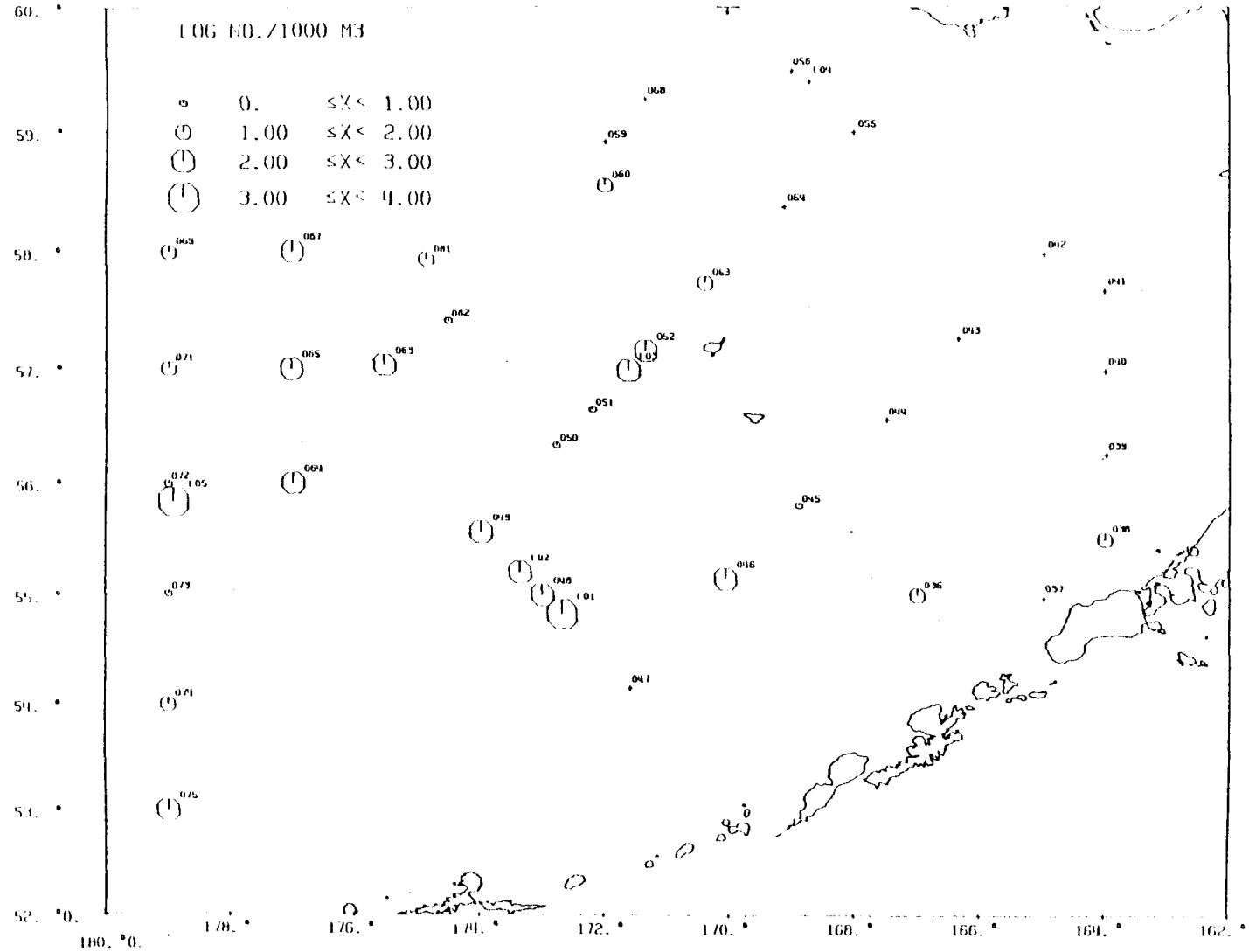

Figure A-3. July, 1979 cephalopod distribution.

Table A-1. Number of stations at which each species was taken (n) and range of number of individuals taken (total no. of stations: 42 in 1977, 55 in 1978 and 40 in 1979).

Species	June 1977		June 1978		July 1979	
	n	range	n	range	n	range
Gonatus onyx	10	1-59	11	1-47	18	1-448
Gonatus tinro	14	1-8	8	1-10	15	1-8
Gonatus madokai	12	1-13	15	1-84	12	1-14
Gonatus type A	4	1-7	5	1-36	3	1-10
Gonatus sp.	6	1-5	11	1-9	7	1-25
Gonatus berryi	-	-	1	4	0	-
Gonatopsis borealis	1	2	3	1-8	3	1-3
Berryteuthis sp.	14	1-5480	0	-	16	1-1141
Unidentified	7	4-301	1	1	3	2-4
Total	27	1-5480	21	1-99	28	1-1175

Table A-2. Abundance and percent composition of cephalopod species taken for the years 1977-1979.

Species	June 1977		June 1978		July 1979	
	n	%	n	%	n	%
Gonatus onyx	164	1.3	99	25.3	951	5.5
Gonatus tinro	39	0.3	27	6.9	115	0.7
Gonatus madokai	68	0.5	150	38.3	296	1.7
Gonatus type A	11	0.1	67	17.1	93	0.5
Gonatus sp.	17	0.1	36	9.2	107	0.6
Gonatus berryi	0	0.0	4	1.0	0	0.0
Gonatopsis borealis	2	0.02	9	2.3	17	0.1
Berryteuthis sp.	12,748	97.6	0	0.0	15,610	90.8
TOTAL	13,049	100	392	100	17,193	100
Unidentified	762		0		0	

APPENDIX B

MORPHOLOGICAL MEASUREMENTS

Table B-1. *Gonatus onyx*. Range, mean and standard deviation of relative morphological measurements.

	MW	FL	FW	BL	BW	ED	T	I	II	III	IV
Adolescent Stage n = 21											
range (mm)	0.51-0.61	0.14-0.18	0.36-0.57	0.19-0.27	0.27-0.34	0.15-0.17	0.45-0.47	0.20-0.29	0.27-0.41	0.23-0.31	0.16-0.24
$\bar{X}$ (mm)	0.56	0.16	0.47	0.23	0.31	0.17	0.46	0.24	0.36	0.28	0.19
S	0.03	0.01	0.06	0.03	0.02	0.01	0.01	0.03	0.04	0.02	0.02
Post-Larval Stage n = 45											
range	0.56-0.67	0.09-0.23	0.29-0.51	0.19-0.27	0.28-0.37	0.14-0.18	0.39-0.73	0.14-0.24	0.17-0.31	0.15-0.25	0.06-0.14
$\bar{X}$	0.61	0.16	0.39	0.23	0.33	0.17	0.56	0.20	0.26	0.22	0.12
S	0.03	0.02	0.07	0.03	0.03	0.01	0.10	0.02	0.03	0.02	0.02
Larval Stage n = 10											
range	0.70-0.79	0.10-0.16	0.30-0.53	0.16-0.27	0.34-0.45	0.14-0.18	0.57-0.83	0.12-0.24	0.16-0.34	0.12-0.23	0.05-0.15
$\bar{X}$	0.74	0.13	0.40	0.23	0.37	0.16	0.71	0.17	0.24	0.17	0.10
S	0.04	0.02	0.10	0.03	0.04	0.01	0.10	0.04	0.06	0.04	0.03

Table B-2. *Gonatus fabricii*. Range, mean and standard deviation of

	MW	FL	FW	HL
Adult Stage n = 5				
range	0.49-0.52	0.33-0.39	0.63-0.71	0.24-0.28
$\bar{X}$	0.51	0.36	0.69	0.26
S	0.012	0.027	0.033	0.016
Adolescent Stage n = 32				
range	0.35-0.55	0.21-0.33	0.55-0.70	0.18-0.32
$\bar{X}$	0.43	0.23	0.63	0.25
S	0.064	0.027	0.043	0.038
Post-Larval Stage n = 12				
range	0.42-0.64	0.09-0.20	0.39-0.64	0.20-0.31
$\bar{X}$	0.56	0.15	0.49	0.28
S	0.100	0.032	0.094	0.034

relative morphological measurements.

HW	ED	T	I	II	III	IV
0.33–0.35	0.21	1.33–1.55	0.40–0.62	0.50–0.71	0.49–0.71	0.51–0.57
0.34	0.21	1.46	0.55	0.62	0.61	0.53
0.010	0.000	0.082	0.092	0.083	0.088	0.026
0.31–0.38	0.18–0.24	0.49–1.55	0.30–0.46	0.33–0.52	0.33–0.51	0.28–0.43
0.34	0.21	0.87	0.36	0.43	0.41	0.34
0.018	0.010	0.365	0.046	0.059	0.056	0.056
0.30–0.42	0.15–0.32	0.41–0.76	0.27–0.46	0.32–0.56	0.29–0.51	0.17–0.37
0.37	0.21	0.59	0.36	0.43	0.39	0.26
0.037	0.047	0.099	0.066	0.090	0.091	0.067

Table B-3. *Gonatus madokai*. Range, mean and standard deviation of relative morphological measurements.

	MW	FL	FW	HL	HW	ED	T	I	II	III	IV
Adolescent Stage n = 5											
range	0.36-0.42	0.32-0.37	0.59-0.64	0.26-0.30	0.22-0.26	0.11-0.12	0.91-0.96	0.64-0.70	0.91-0.96	0.93-0.96	0.52-0.55
$\bar{X}$	0.39	0.35	0.62	0.28	0.24	0.11	0.94	0.68	0.94	0.95	0.54
S	0.022	0.019	0.025	0.016	0.015	0.006	0.027	0.023	0.019	0.011	0.013
Post-Larval Stage n = 13											
range	0.33-0.44	0.14-0.31	0.47-0.61	0.25-0.28	0.24-0.27	0.11-0.12	0.44-0.66	0.32-0.57	0.71-0.84	0.71-0.84	0.13-0.39
$\bar{X}$	0.38	0.24	0.53	0.27	0.26	0.11	0.52	0.47	0.77	0.79	0.26
S	0.027	0.068	0.049	0.013	0.017	0.005	0.077	0.092	0.044	0.046	0.095
Larval Stage n = 29											
range	0.49-0.86	0.05-0.16	0.26-0.39	0.21-0.28	0.25-0.48	0.12-0.17	0.70-1.15	0.17-0.29	0.34-0.78	0.15-0.67	0.04-0.11
$\bar{X}$	0.71	0.10	0.32	0.25	0.37	0.16	0.94	0.20	0.48	0.41	0.08
S	0.091	0.036	0.039	0.023	0.045	0.017	0.119	0.032	0.140	0.125	0.021

Table B-4. *Gonatus* sp. Range, mean and standard deviation of relative morphological measurements.

	MW	FL	FW	HL	HW	ED	T	I	II	III	IV
Adolescent Stage n = 12											
range	0.42-0.45	0.13-0.35	0.43-0.87	0.22-0.24	0.27-0.34	0.15-0.21	0.37-0.49	0.31-0.47	0.37-0.59	0.31-0.55	0.26-0.47
$\bar{X}$	0.44	0.25	0.63	0.23	0.31	0.20	0.43	0.39	0.44	0.41	0.34
S	0.011	0.063	0.133	0.009	0.023	0.022	0.041	0.052	0.060	0.067	0.061
Post-Larval Stage n = 23											
range	0.35-0.61	0.07-0.31	0.24-0.54	0.19-0.33	0.30-0.44	0.14-0.22	0.41-0.75	0.19-0.59	0.23-0.55	0.21-0.46	0.12-0.27
$\bar{X}$	0.52	0.15	0.41	0.25	0.34	0.17	0.59	0.26	0.35	0.30	0.18
S	0.071	0.058	0.079	0.036	0.047	0.025	0.092	0.065	0.087	0.072	0.047
Larval Stage n = 6											
range	0.51-0.79	0.08-0.15	0.26-0.36	0.22-0.40	0.33-0.50	0.14-0.21	0.47-0.77	0.19-0.41	0.29-0.53	0.20-0.45	0.06-0.30
$\bar{X}$	0.62	0.12	0.34	0.28	0.38	0.17	0.73	0.28	0.36	0.31	0.14
S	0.114	0.026	0.078	0.074	0.065	0.030	0.029	0.101	0.111	0.095	0.085

Table B-5. *Gonatus* type A. Range, mean and standard deviation of relative morphological measurements.

	MW	FL	FW	HL	HW	ED	T	I	II	III	IV
Adolescent Stage n = 13											
range	0.28-0.36	0.21-0.27	0.33-0.49	0.19-0.23	0.17-0.21	0.11-0.12	0.39-0.43	0.29-0.38	0.37-0.47	0.34-0.46	0.17-0.30
$\bar{X}$	0.31	0.23	0.43	0.20	0.19	0.11	0.40	0.32	0.43	0.39	0.20
S	0.026	0.029	0.048	0.019	0.014	0.009	0.063	0.029	0.039	0.042	0.044
Post-Larval Stage n = 11											
range	0.29-0.37	0.18-0.31	0.33-0.55	0.14-0.23	0.19-0.24	0.11-0.14	0.42-0.50	0.17-0.35	0.27-0.46	0.28-0.43	0.06-0.21
$\bar{X}$	0.35	0.20	0.40	0.22	0.21	0.12	0.46	0.25	0.37	0.34	0.14
S	0.029	0.044	0.064	0.031	0.019	0.009	0.025	0.059	0.058	0.050	0.038
Larval Stage n = 3											
range	0.39-0.50	0.09-0.27	0.31-0.47	0.17-0.24	0.22-0.25	0.10-0.15	0.37-0.65	0.19-0.31	0.37-0.41	0.21-0.43	0.12-0.14
$\bar{X}$	0.44	0.20	0.38	0.21	0.24	0.12	0.53	0.25	0.39	0.32	0.13
S	0.055	0.095	0.083	0.038	0.015	0.025	0.143	0.060	0.028	0.110	0.010

APPENDIX C

SYSTEMATIC ILLUSTRATIONS

(plates 1-42)

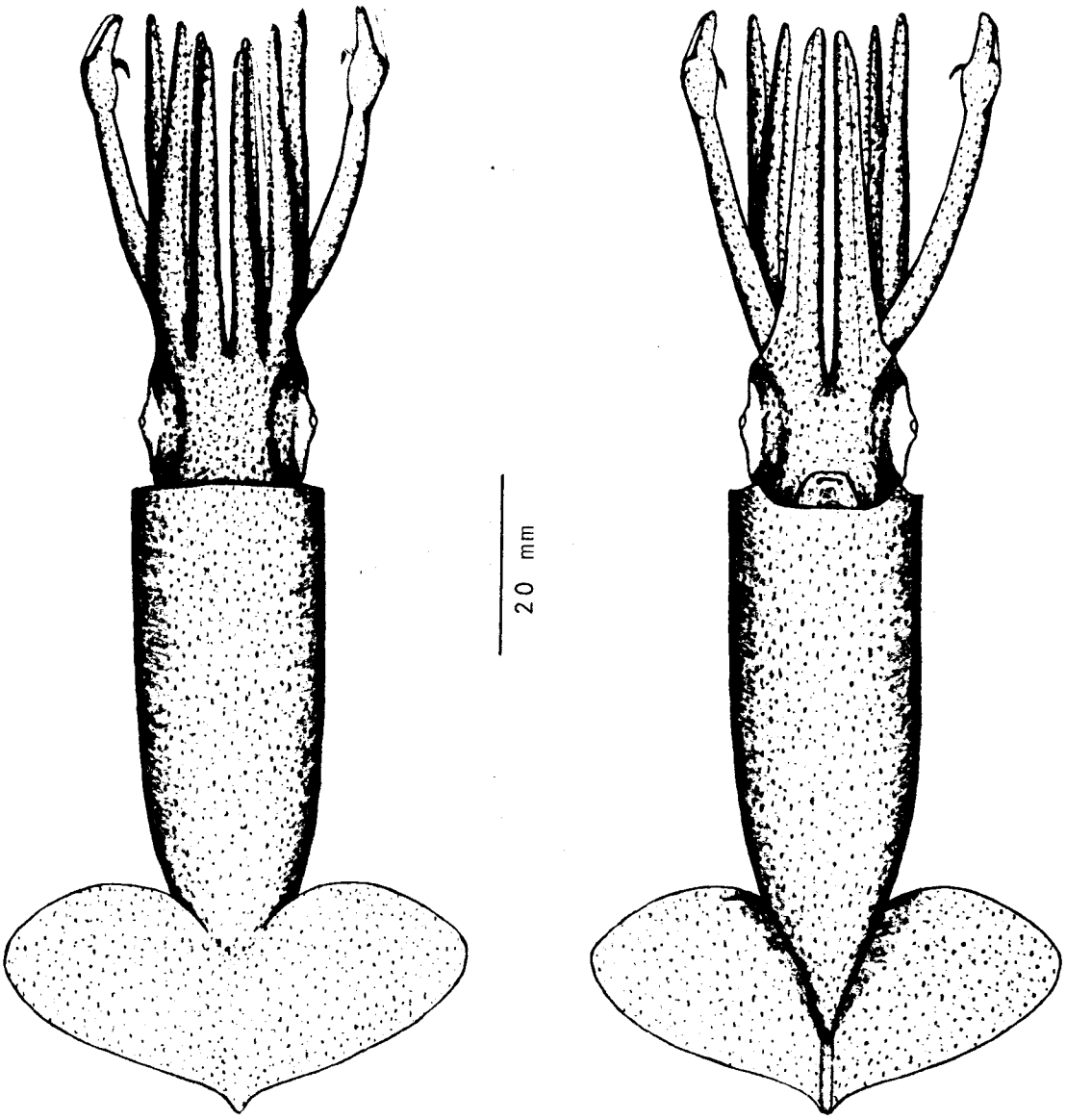

Plate 1. *Gonatus onyx*, adult stage: dorsal and ventral view of a 67 mm DML specimen.

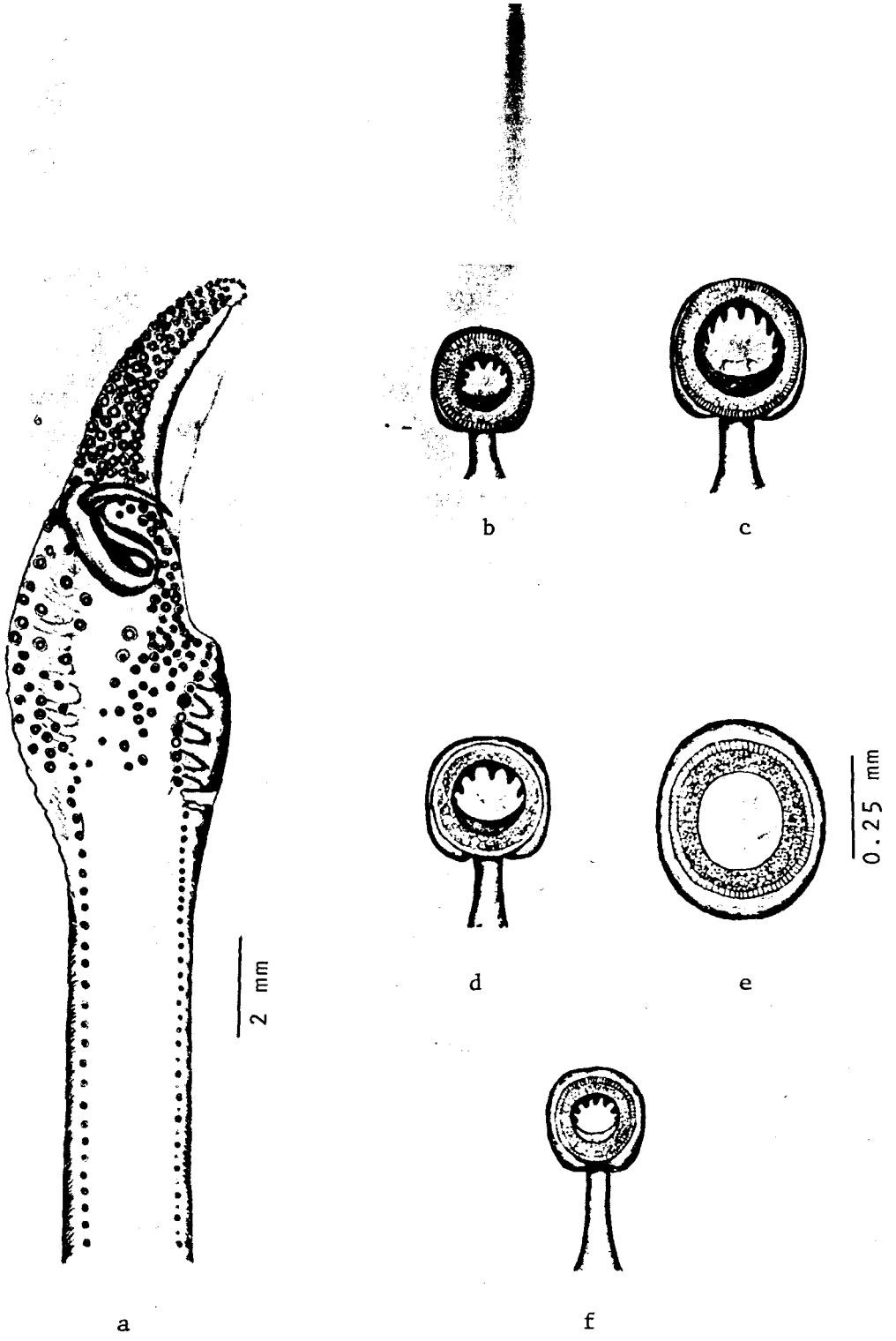

Plate 2. *Gonatus onyx*, adult stage: (a) tentacle, (b) largest sucker from dactylus, (c) largest ventral-marginal zone sucker, (d) largest median zone sucker, (e) largest locking zone sucker and (f) largest dorsal-marginal zone sucker.

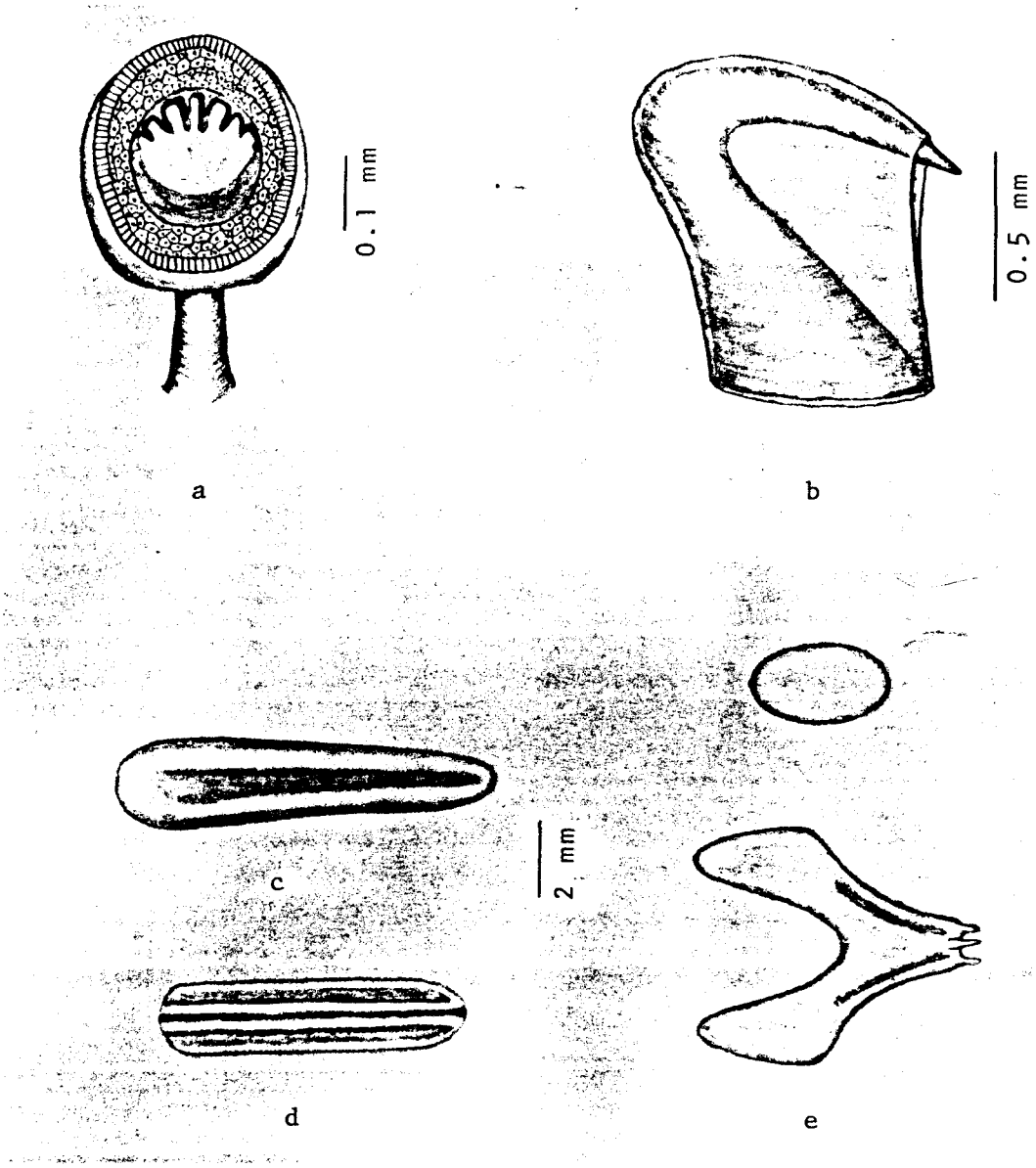

Plate 3. *Gonatus onyx*, adult stage: (a) largest lateral sucker from arm II, (b) largest median hook from arm II, (c) funnel locking cartilage, (d) nuchal cartilage and (e) funnel organ.

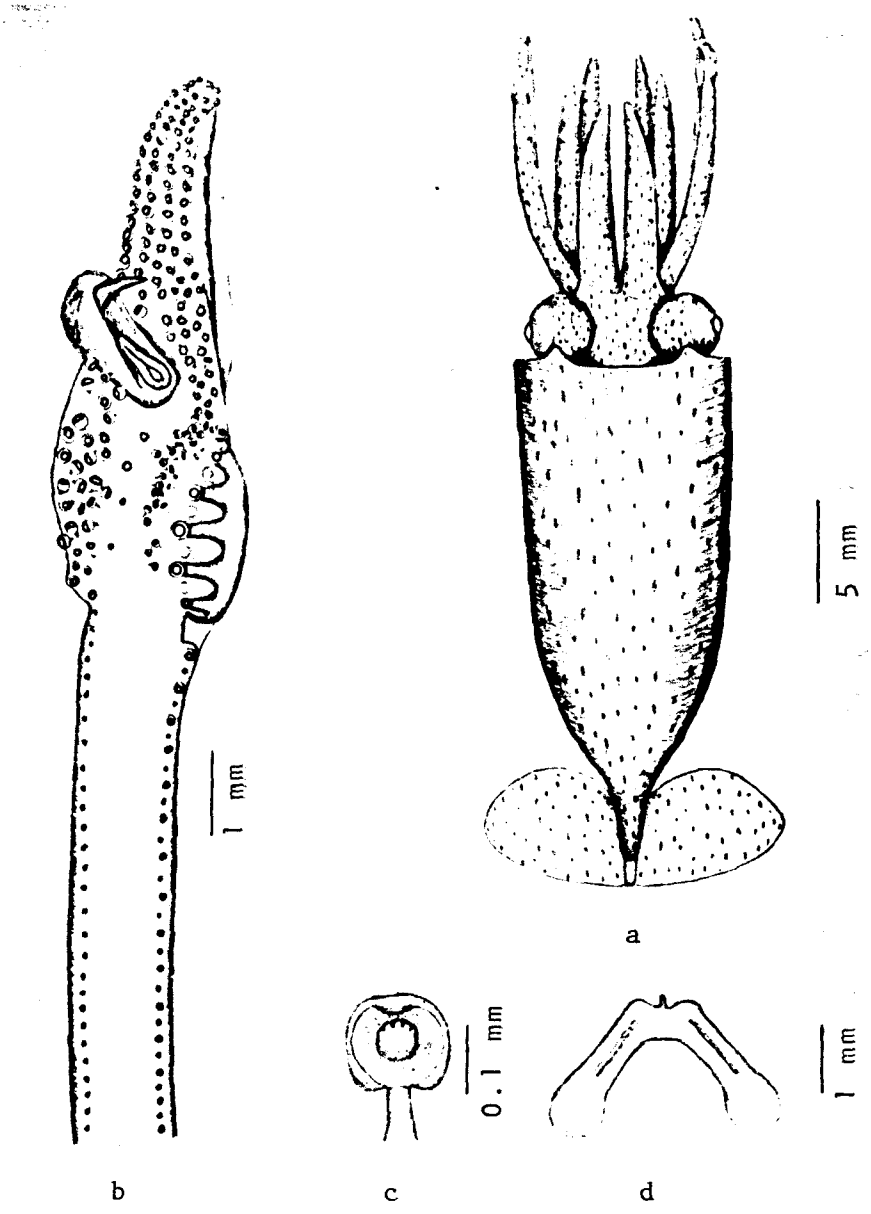

Plate 4. *Gonatus onyx*, late adolescent phase: (a) ventral view of a 25 mm DML specimen, (b) tentacle, (c) median row sucker of arm II and (d) dorsal pad of funnel organ.

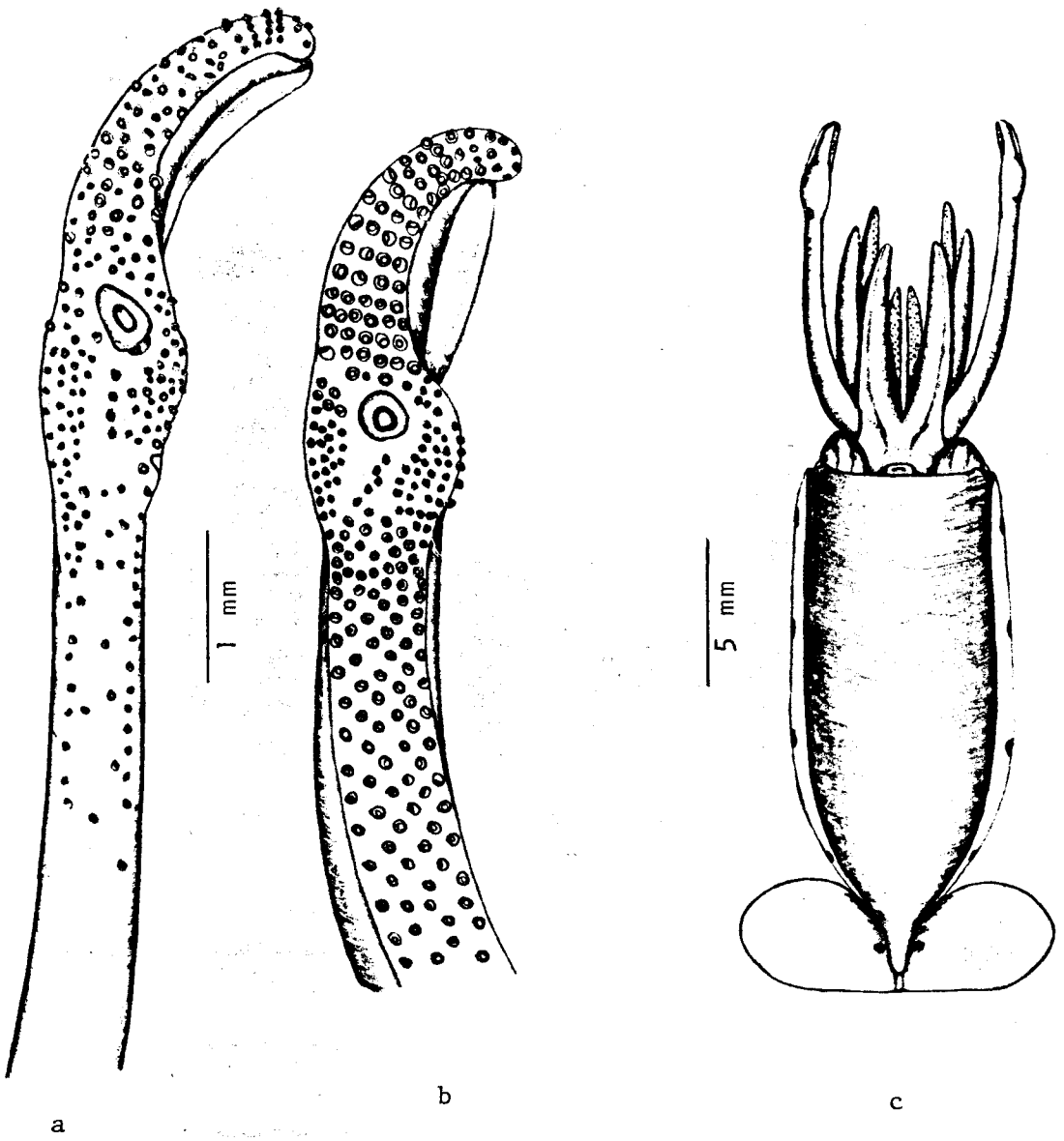

Plate 5. *Gonatus onyx*, early adolescent phase: (a) tentacle of a 17 mm DML specimen, (b) tentacle from a 12 mm DML specimen and (c) ventral view of a 17 mm DML specimen.

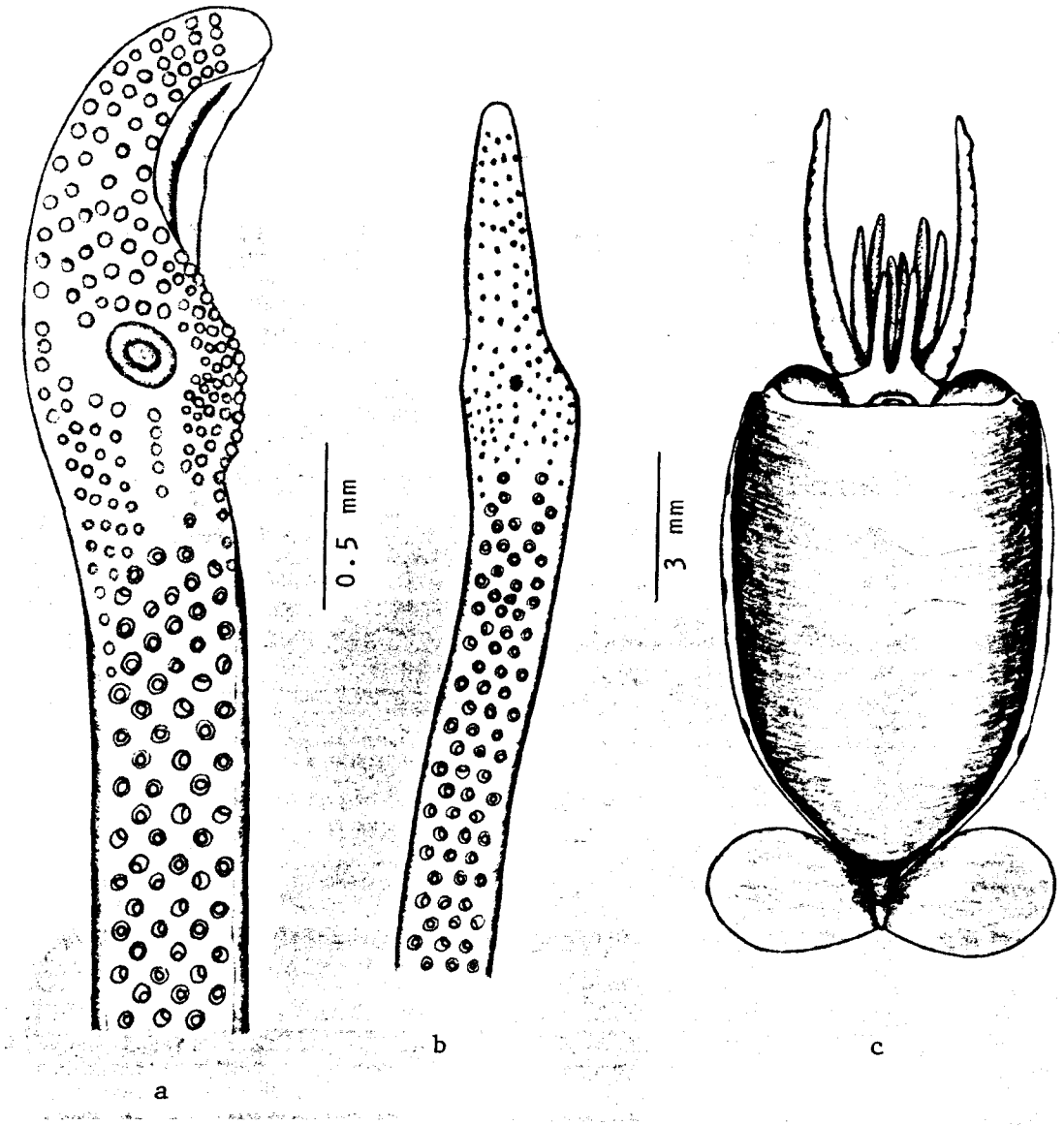

Plate 6. *Gonatus onyx*, post larval stage: (a) tentacle of an 11 mm DML specimen, (b) tentacle of an 8 mm DML specimen and (c) ventral view of an 11 mm DML specimen.

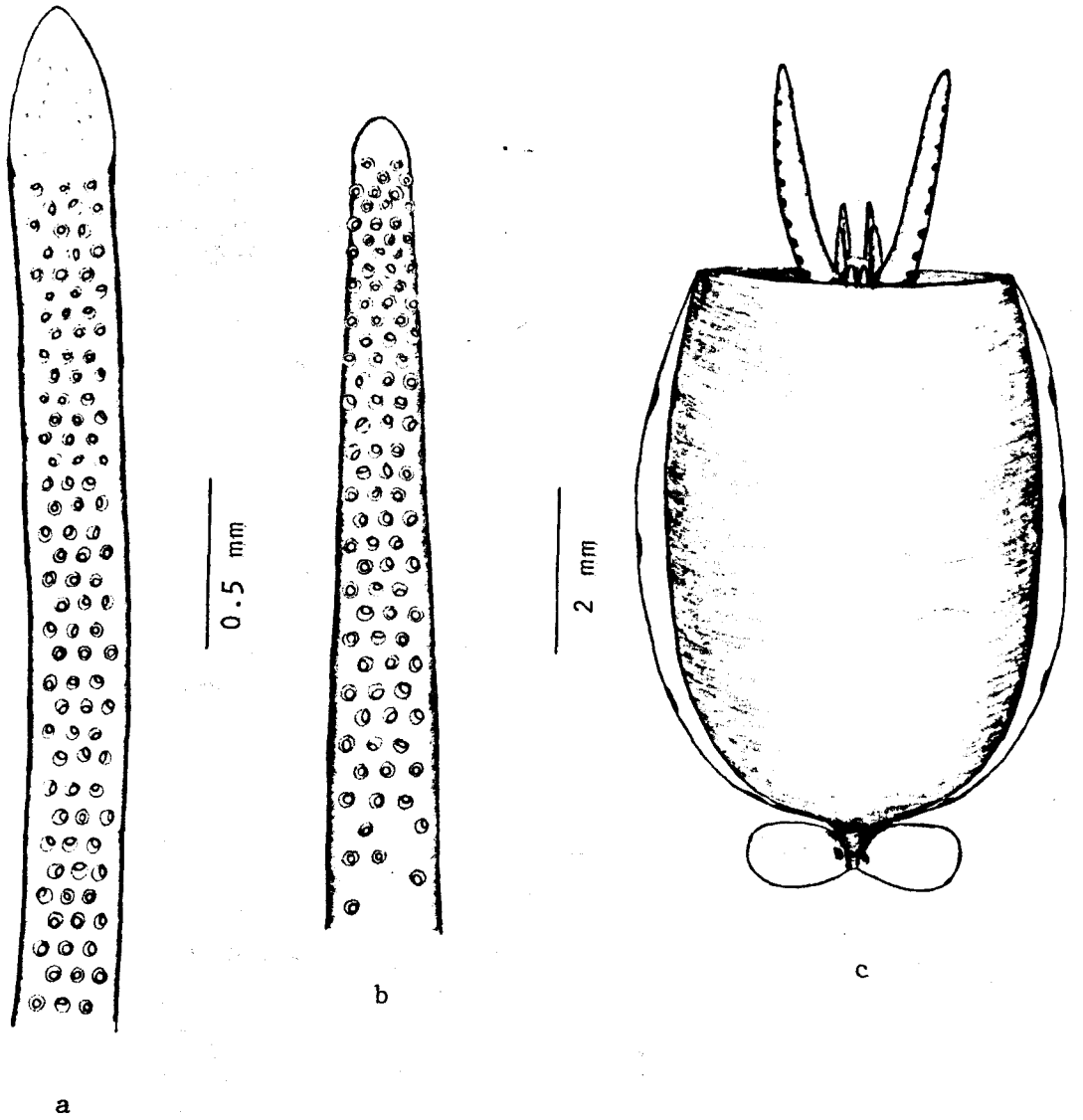

Plate 7. *Gonatus onyx*, larval stage: (a) tentacle from an 8 mm DML specimen, (b) tentacle from a 6 mm DML specimen and (c) ventral view of a 6 mm DML specimen.

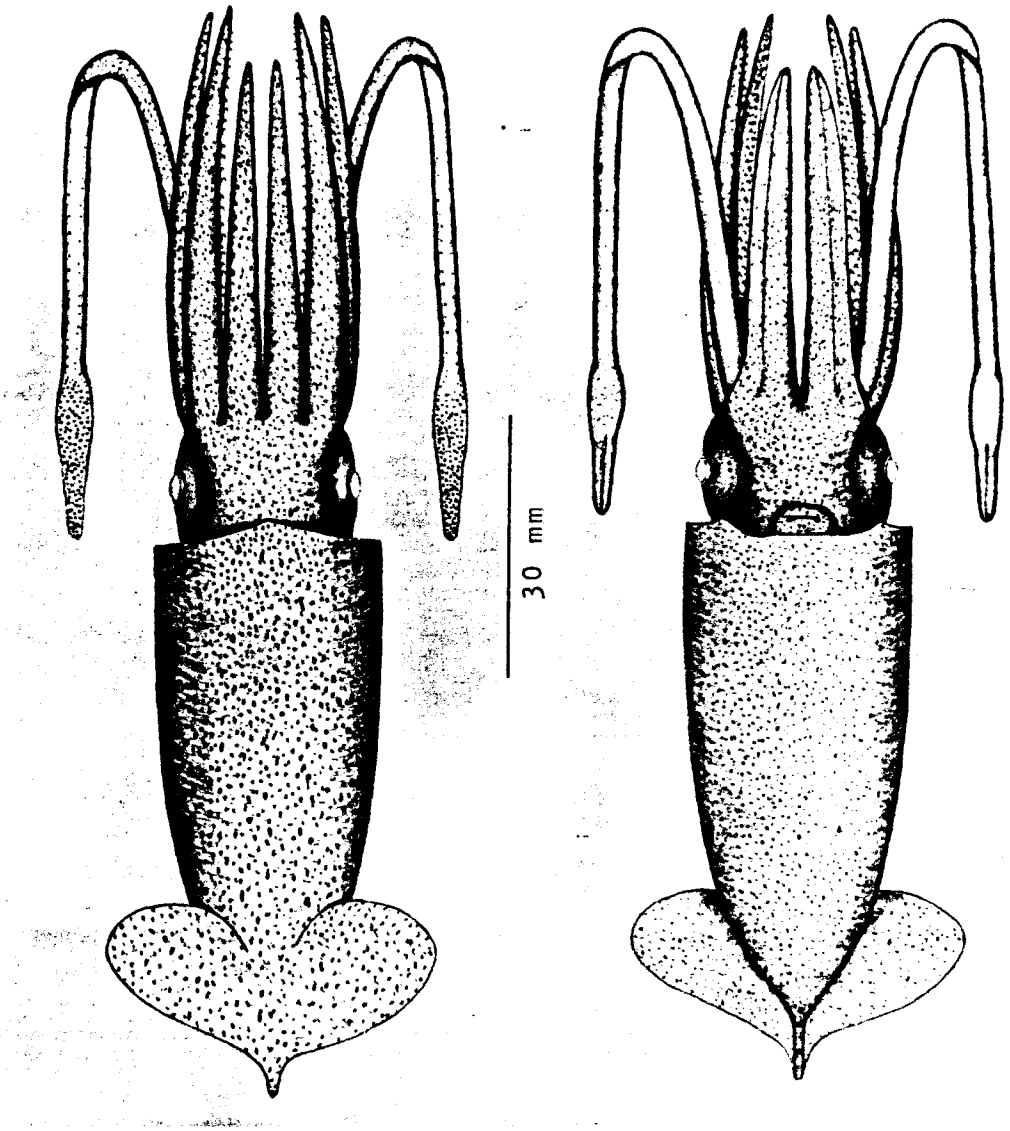

Plate 8. *Gonatus tinro*, adult stage: dorsal and ventral view of a 67 mm DML specimen.

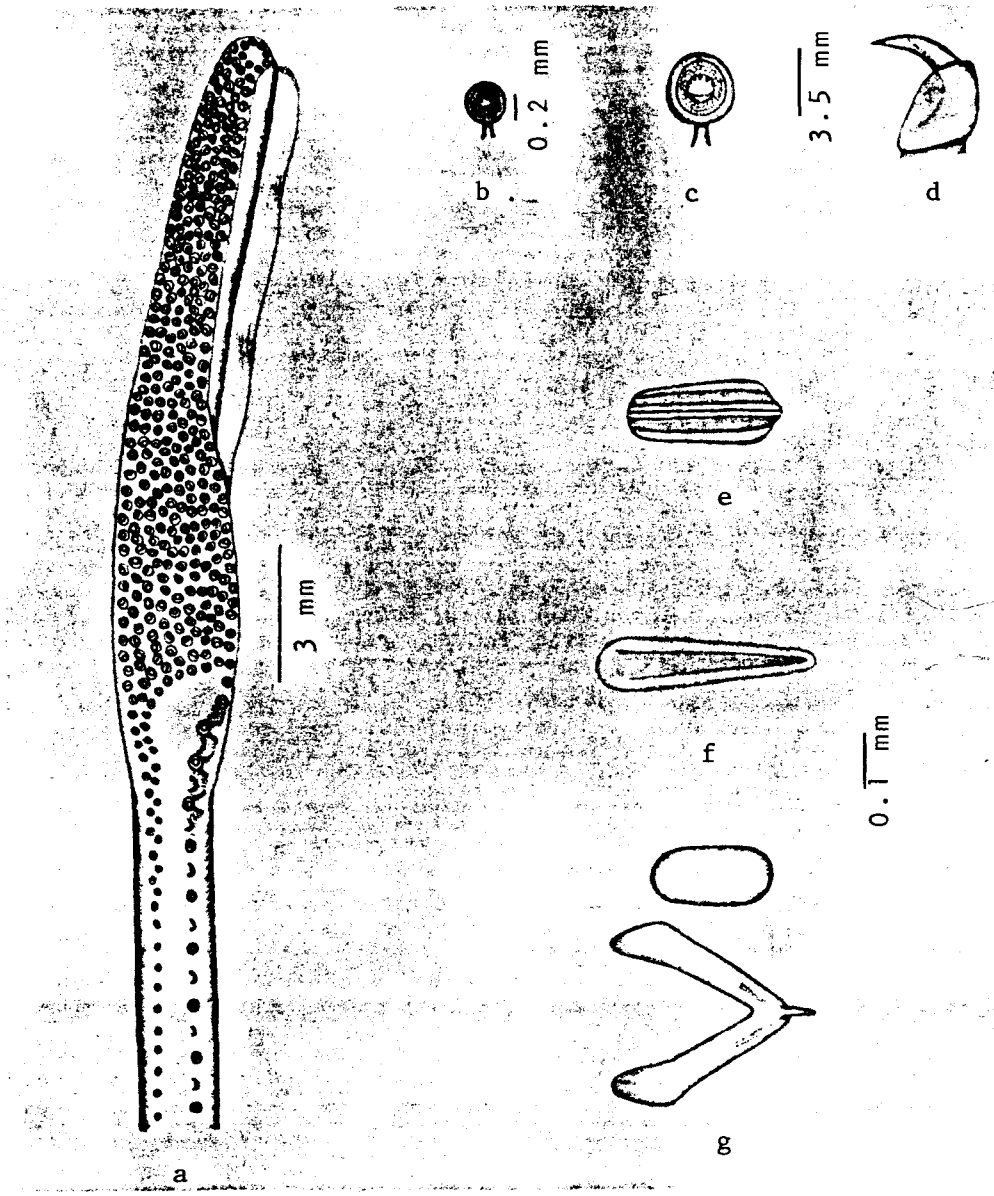

Plate 9. *Gonatus tinro*, adult stage: (a) tentacle, (b) tentacular club sucker, (c) lateral sucker from arm II, (d) median hook from arm II, (e) nuchal cartilage, (f) funnel locking cartilage and (g) funnel organ.

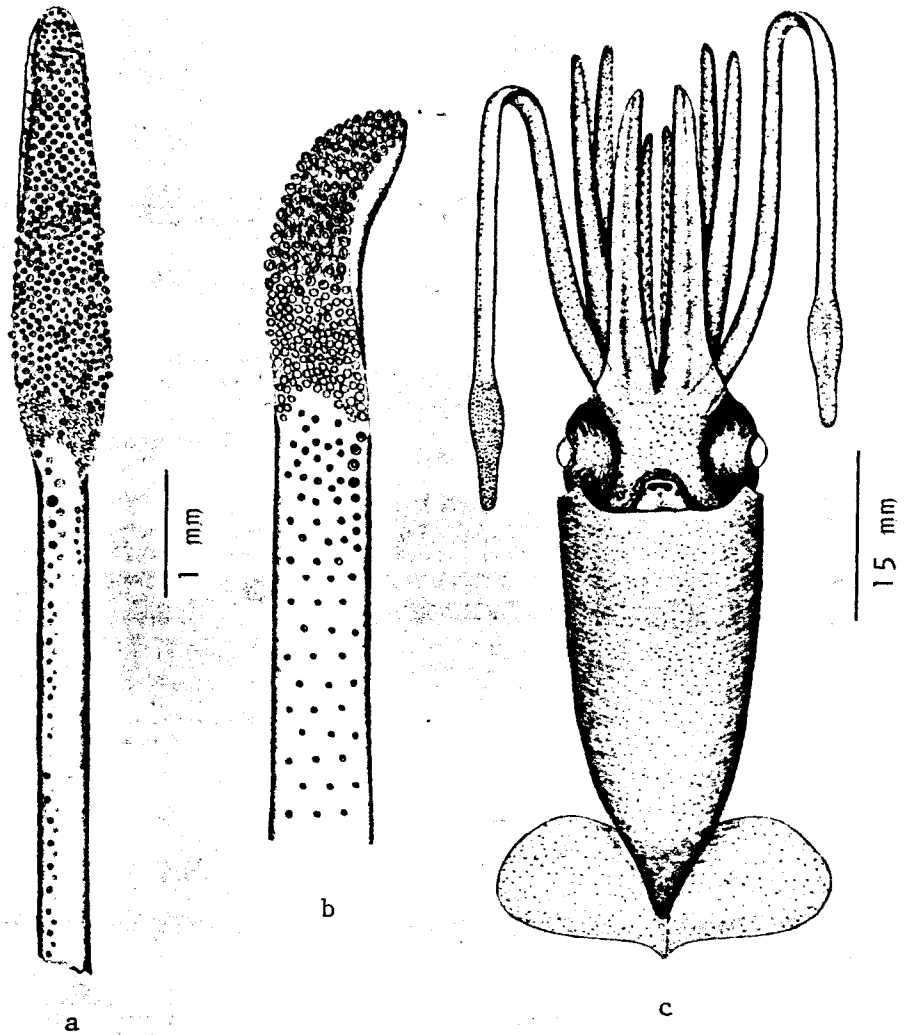

Plate 10. *Gonatus tinro*, adolescent stage: (a) tentacle from a 42 mm DML specimen, (b) tentacle from a 33 mm DML specimen and (c) ventral view of a 42 mm DML specimen.

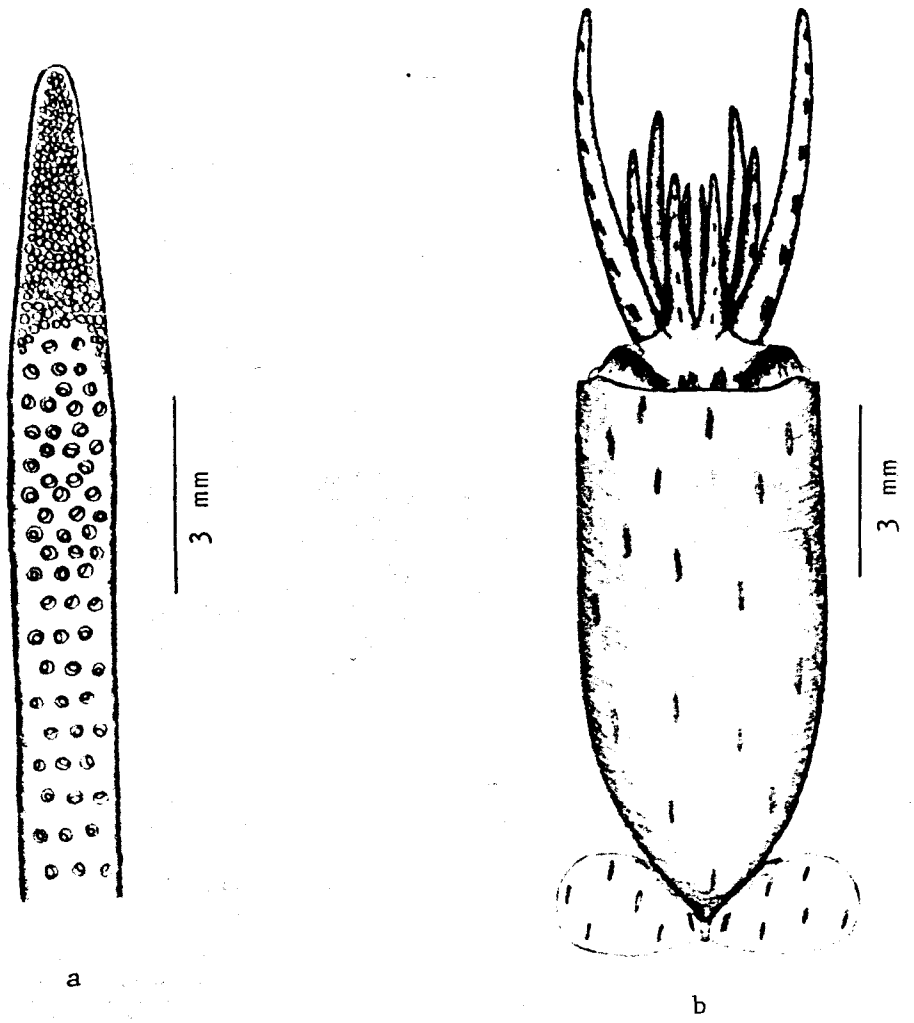

Plate 11. *Gonatus tinro*, post larval stage: (a) tentacle of a 10 mm DML specimen and (b) ventral view of a 10 mm DML specimen.

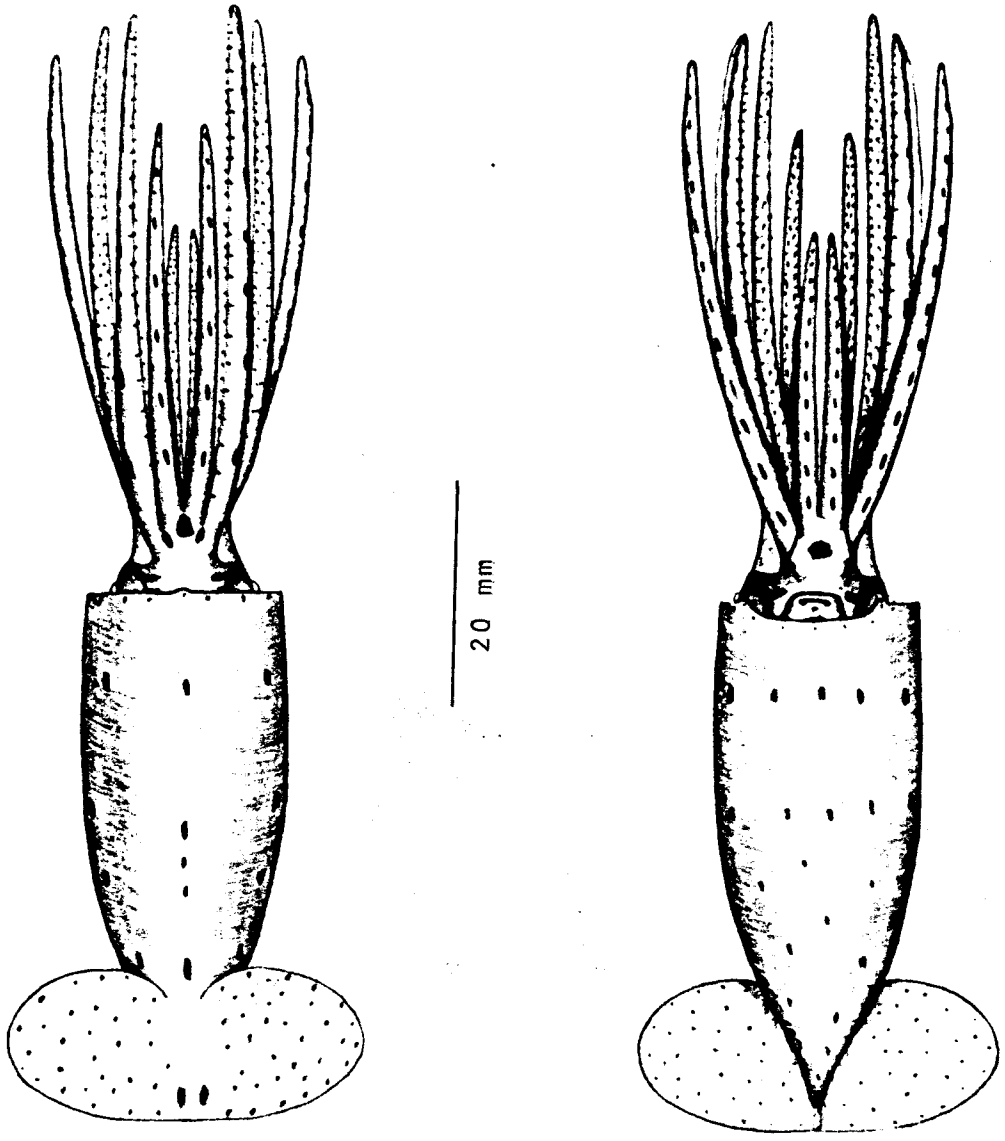

Plate 12. *Gonatus madokai*, adolescent stage: dorsal and ventral view of a 42 mm DML specimen.

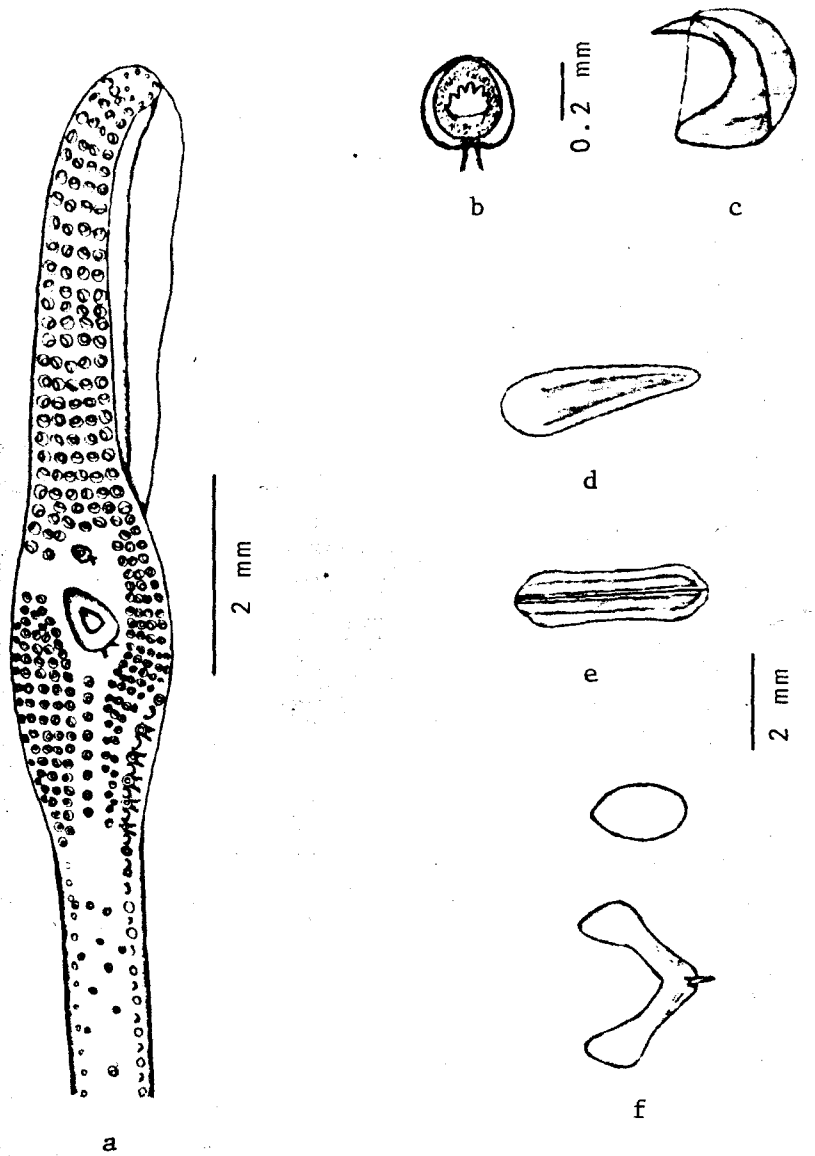

Plate 13. *Gonatus madokai*, adolescent stage: (a) tentacle, (b) largest lateral sucker from arm III, (c) largest median hook from arm III, (d) funnel locking cartilage, (e) nuchal cartilage and (f) funnel organ.

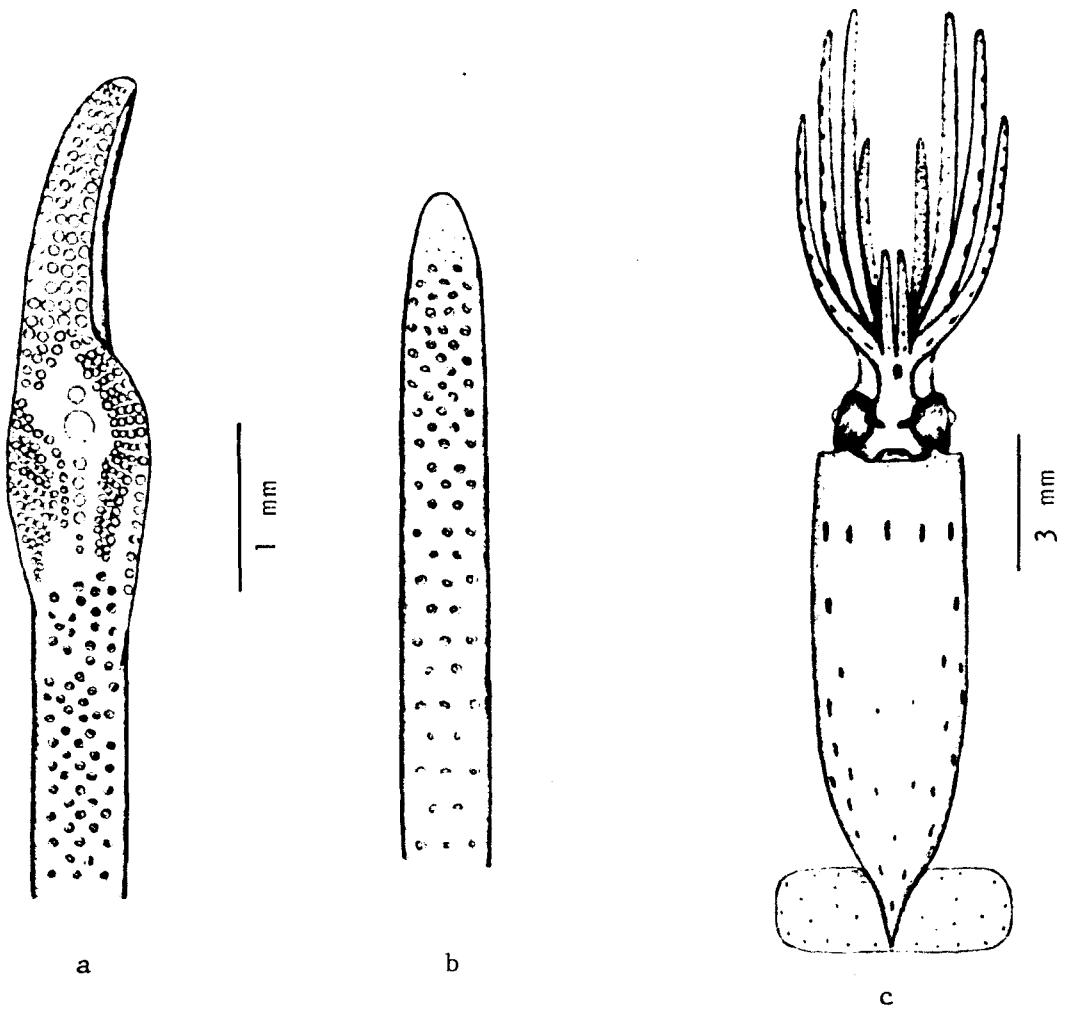

Plate 14. *Gonatus madokai*, post-larval stage: (a) tentacle from 26 mm DML specimen, (b) tentacle from 11 mm DML specimen and (c) ventral view of 11 mm DML specimen.

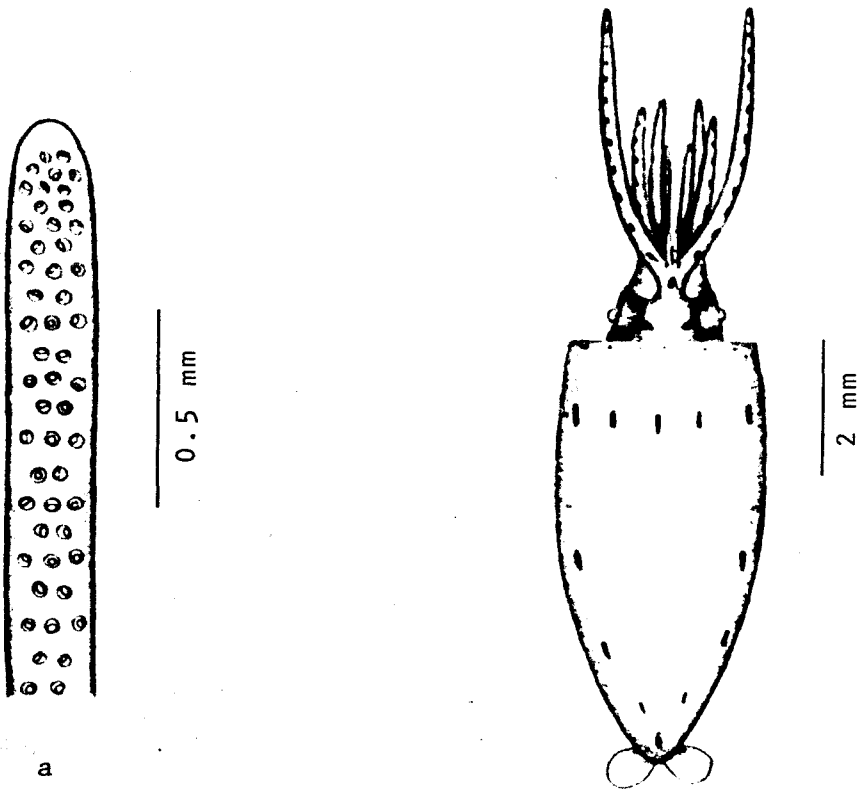

Plate 15. *Gonatus madokai*, larval stage: (a) tentacle and (b) ventral view of a 5 mm DML specimen.

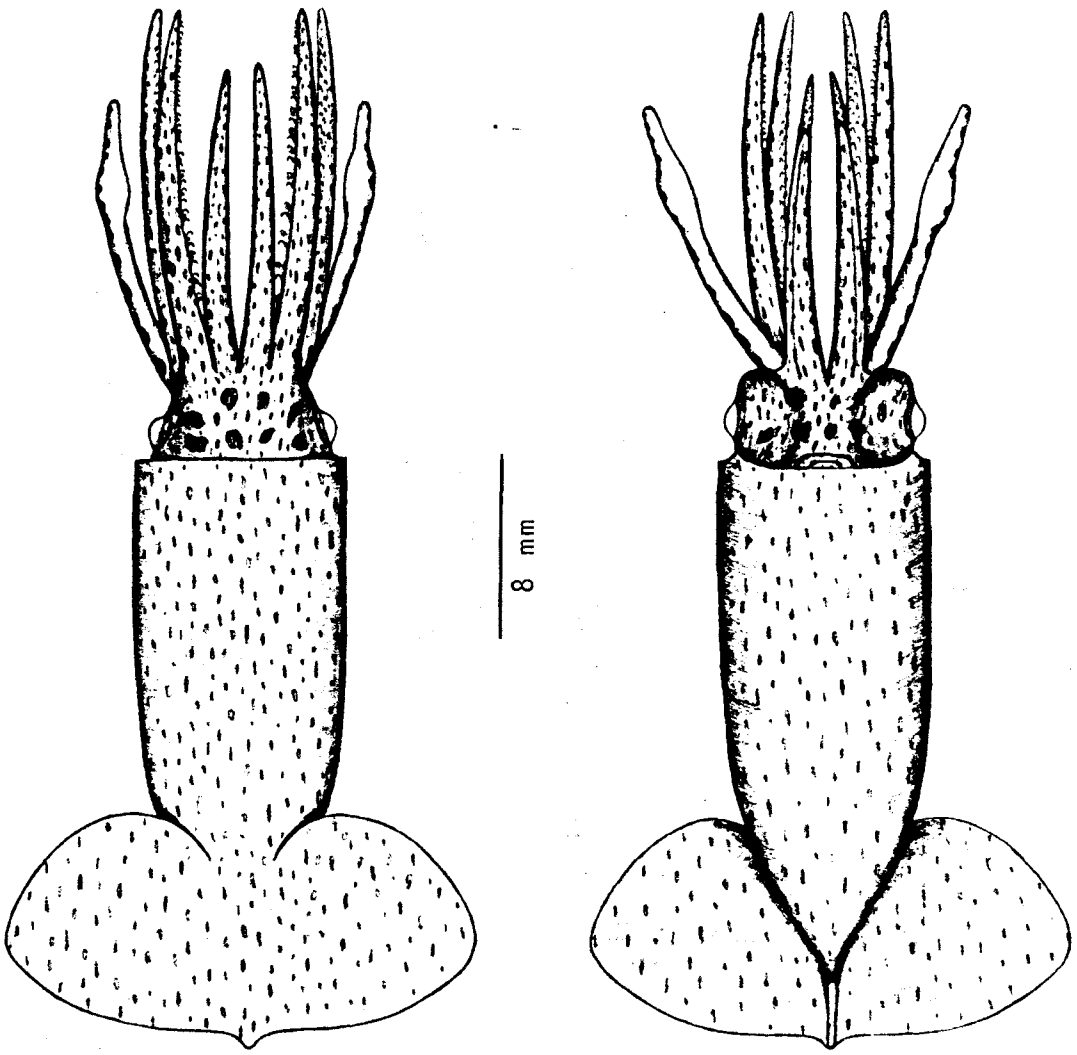

Plate 16. *Gonatus berryi*, adolescent stage: dorsal and ventral view of a 27 mm DML specimen.

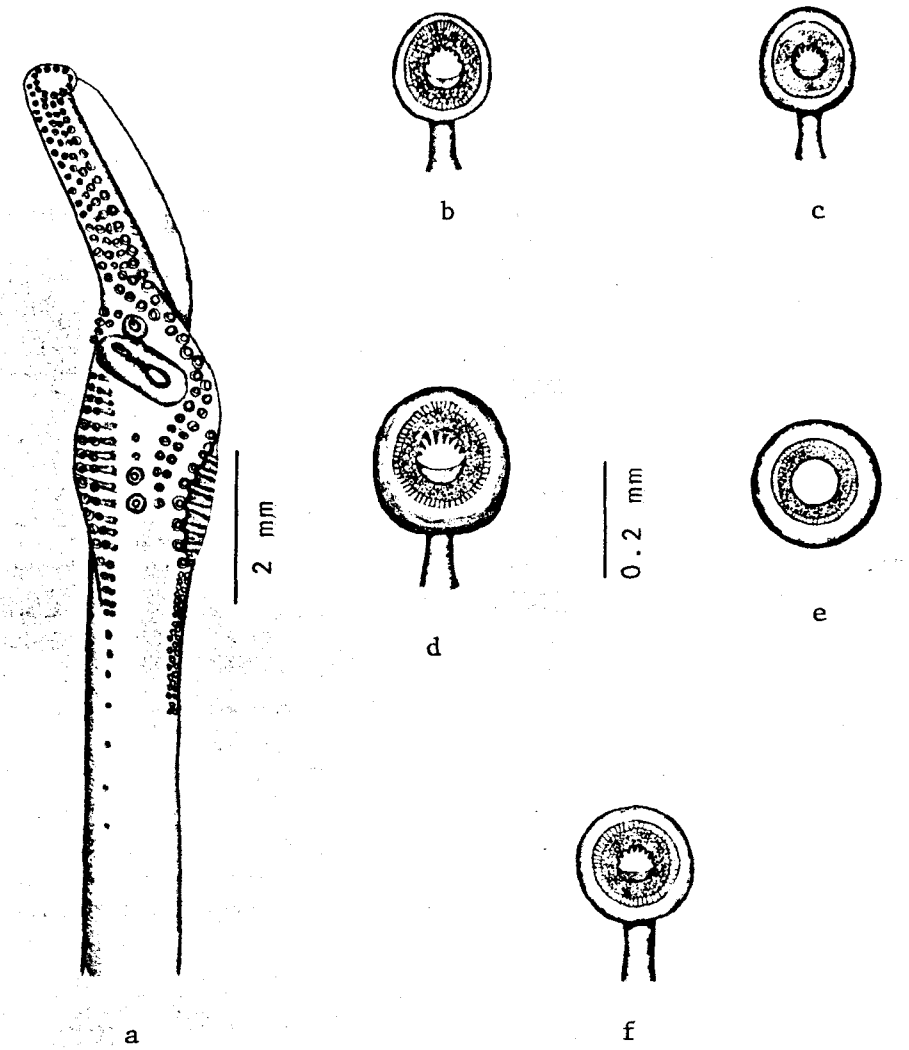

Plate 17. *Gonatus berryi*, adolescent stage: (a) tentacle of a 27 mm DML specimen, (b) largest sucker from dactylus, (c) largest ventral-marginal zone sucker, (d) largest median zone sucker, (e) locking zone sucker and (f) largest dorsal-marginal zone sucker.

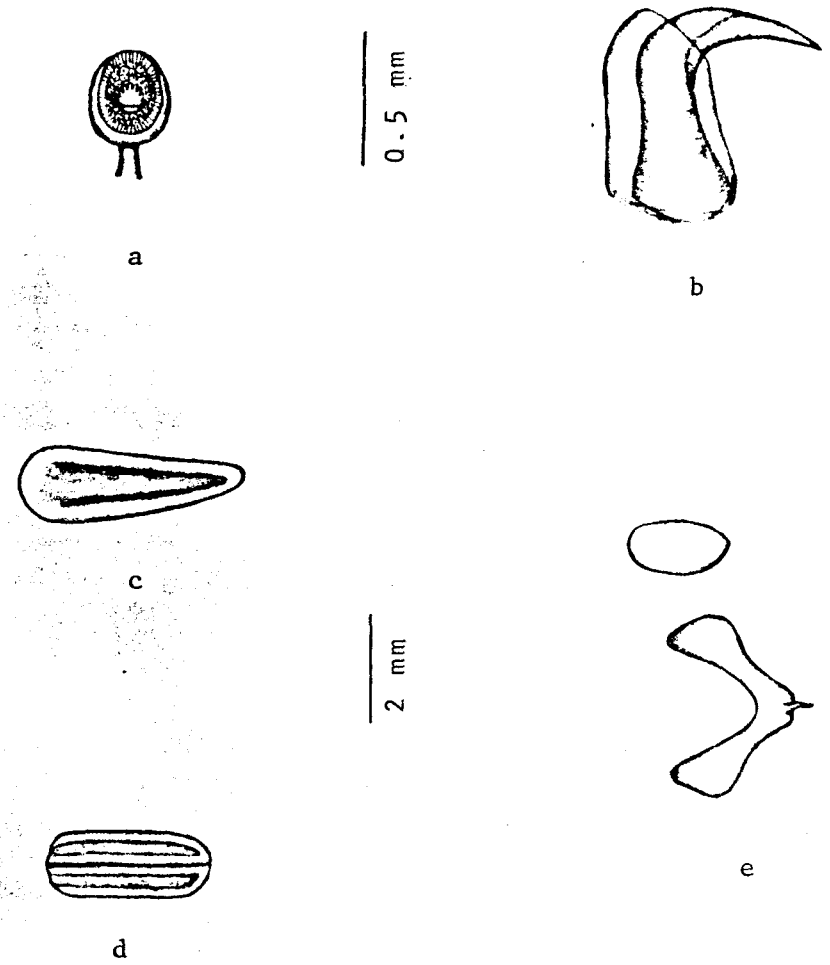

Plate 18. *Gonatus berryi*, adolescent stage: (a) largest lateral sucker from arm II, (b) largest median hook from arm II, (c) funnel locking cartilage, (d) nuchal cartilage and (e) funnel organ.

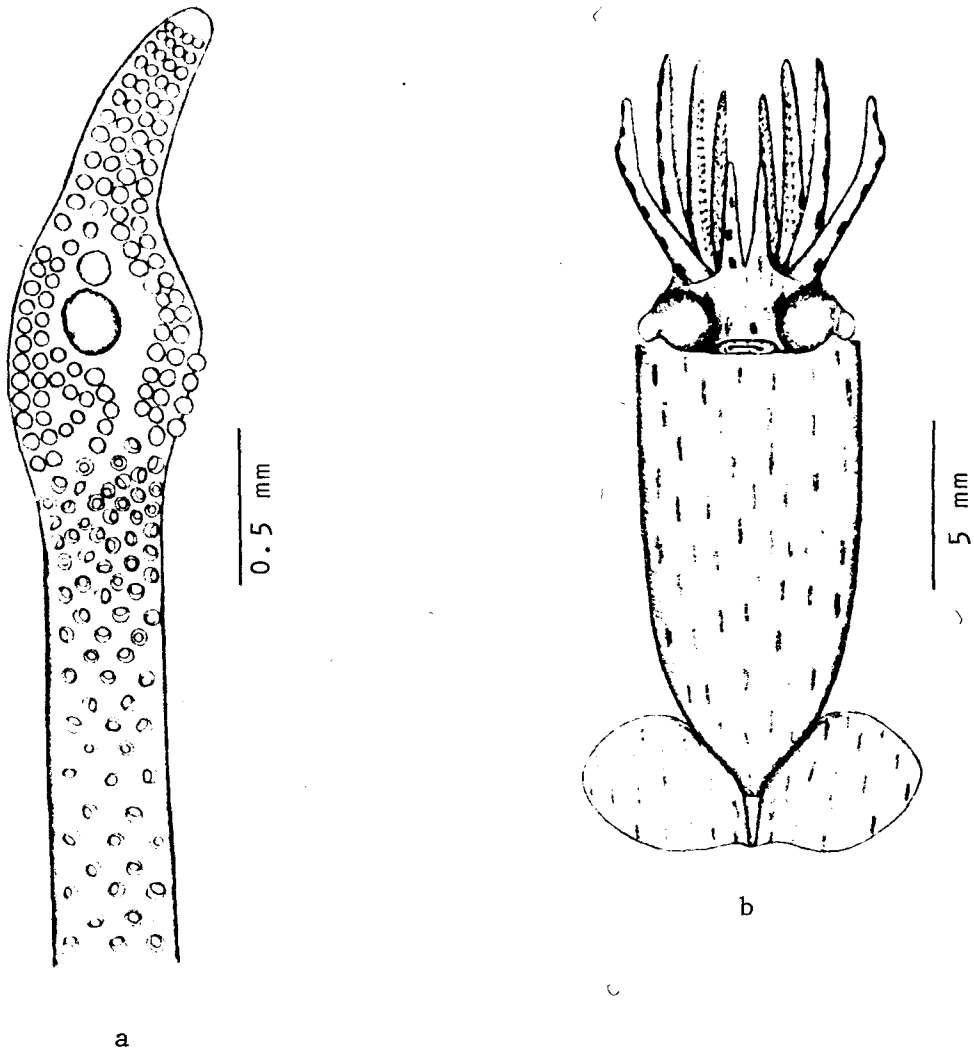

Plate 19. *Gonatus berryi*, post-larval stage: (a) tentacle and (b) ventral view of a 12 mm DML specimen.

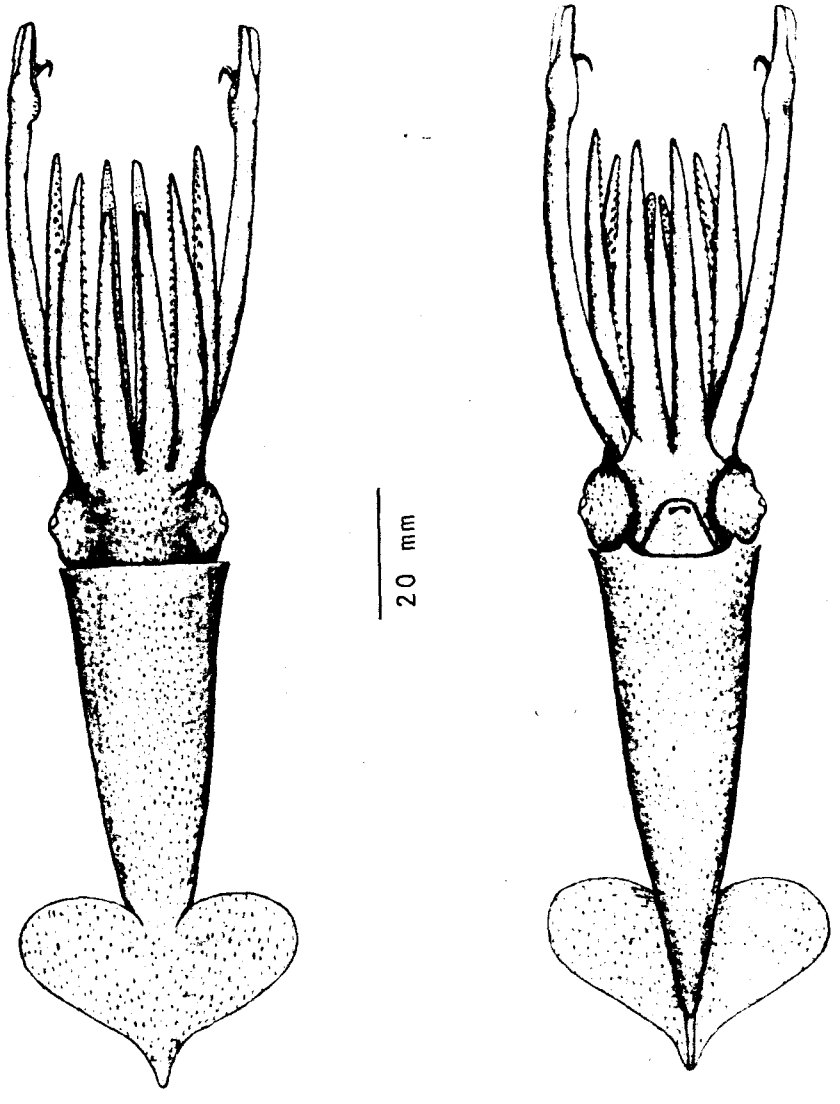

Plate 20. *Gonatus* sp., adult stage: dorsal and ventral view of an 80 mm DML specimen.

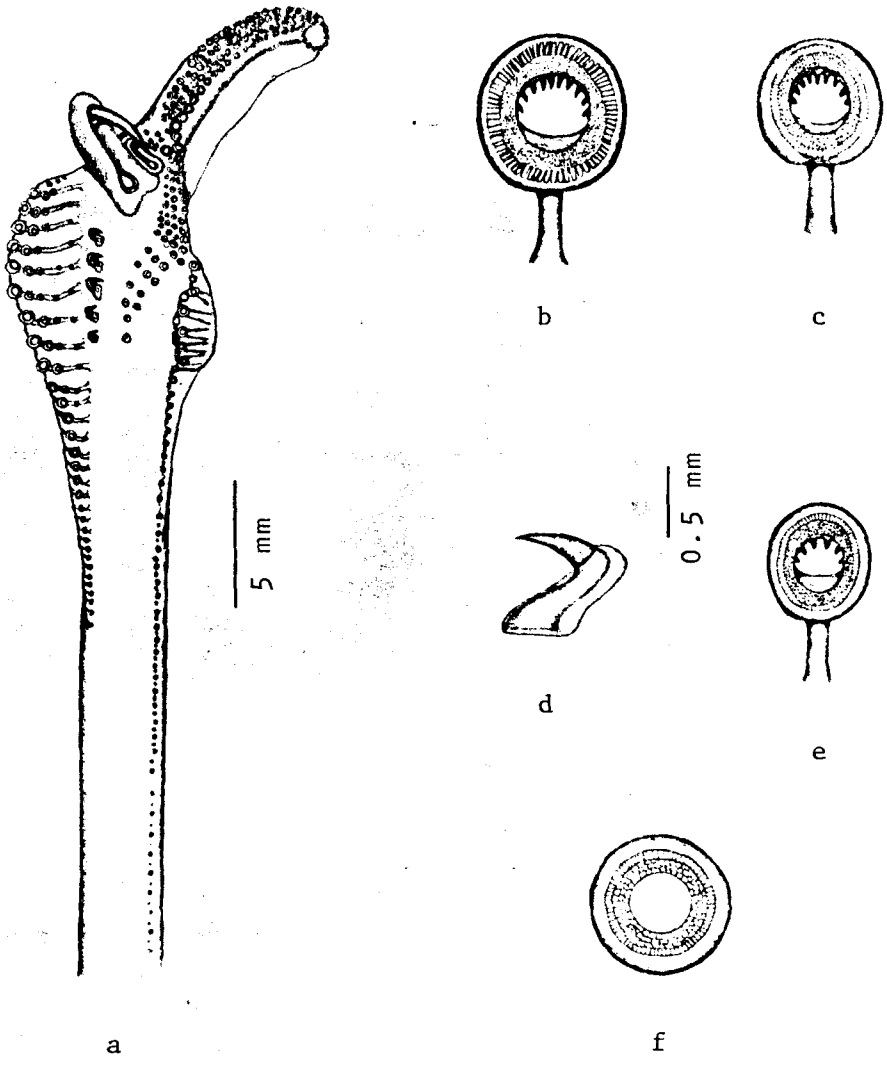

Plate 21. *Gonatus* sp., adult stage: (a) tentacle from an 80 mm DML specimen, (b) largest sucker from the dactylus, (c) largest sucker from the ventral marginal zone, (d) largest proximal hook from the median zone, (e) largest sucker from the dorsal-marginal zone and (f) largest sucker from the locking zone.

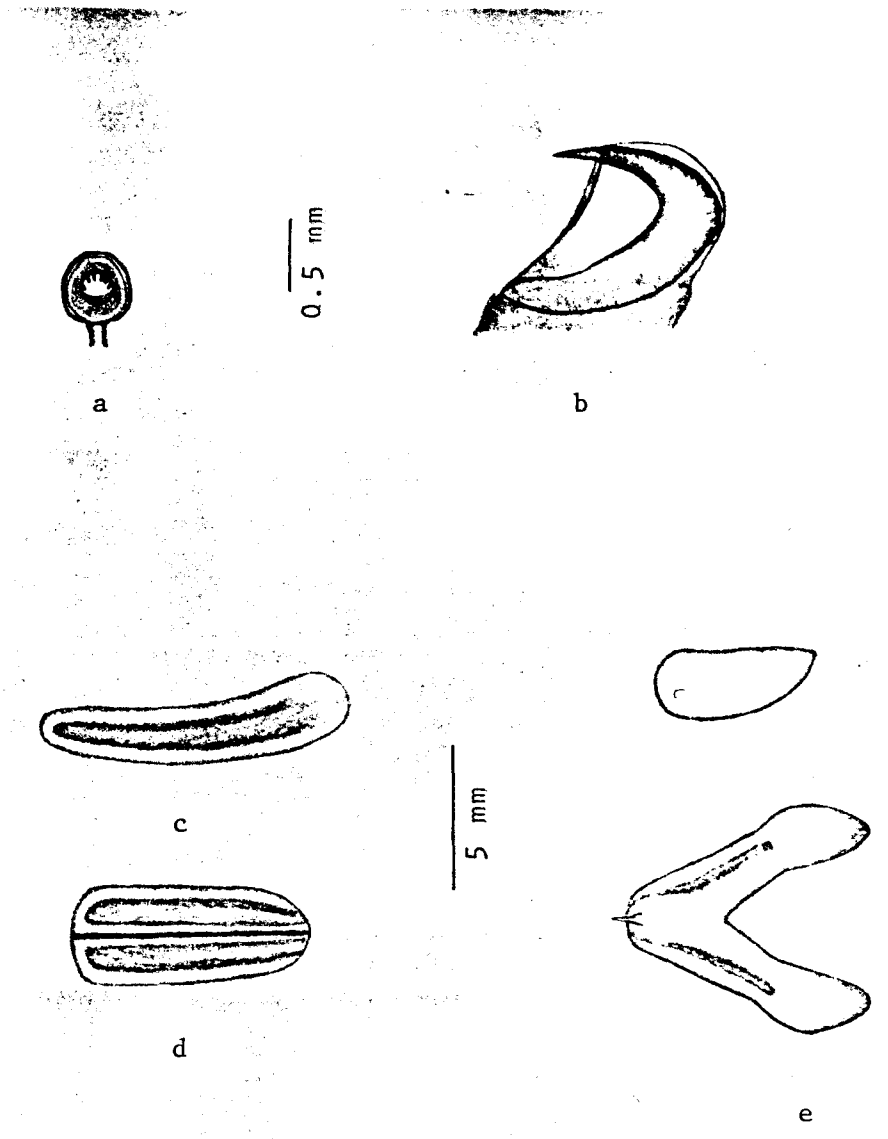

Plate 22. *Gonatus* sp., adult stage: (a) largest lateral sucker from arm III, (b) largest median hook from arm III, (c) funnel locking cartilage, (d) nuchal cartilage and (e) funnel organ.

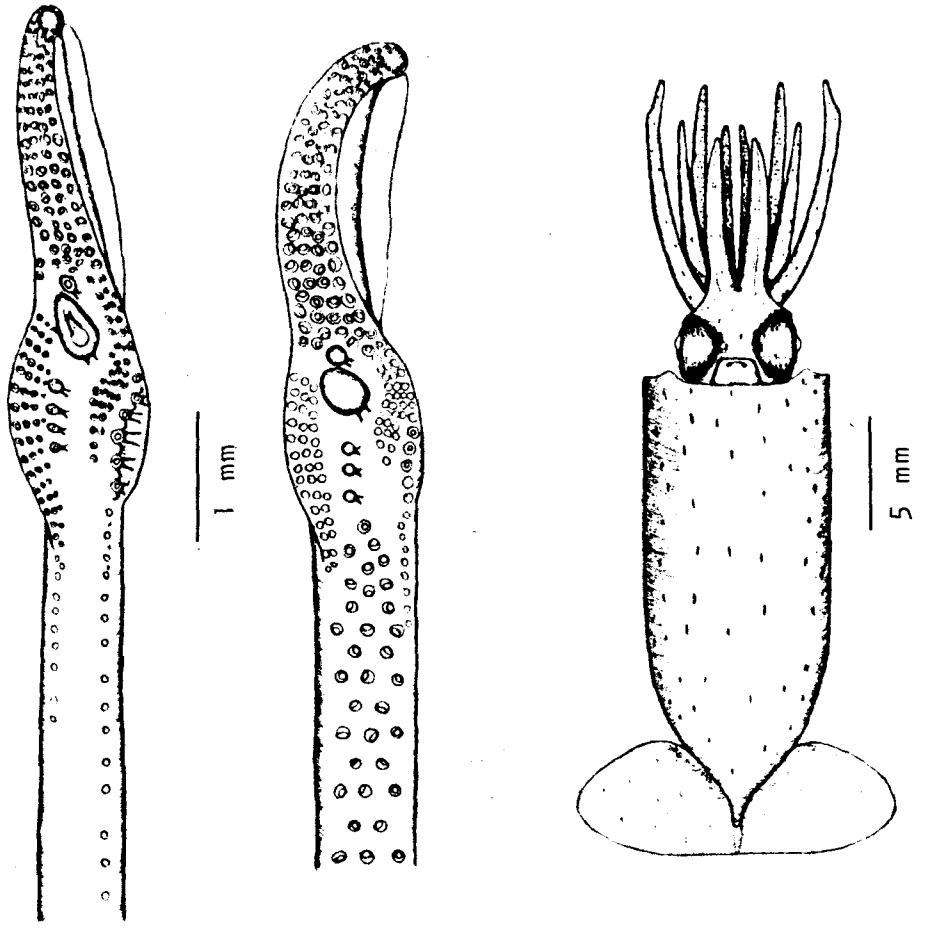

Plate 23. *Gonatus* sp., adolescent stage: (a) tentacle from a 22 mm DML specimen, (b) tentacle from a 16 mm DML specimen and (c) ventral view of a 22 mm DML specimen.

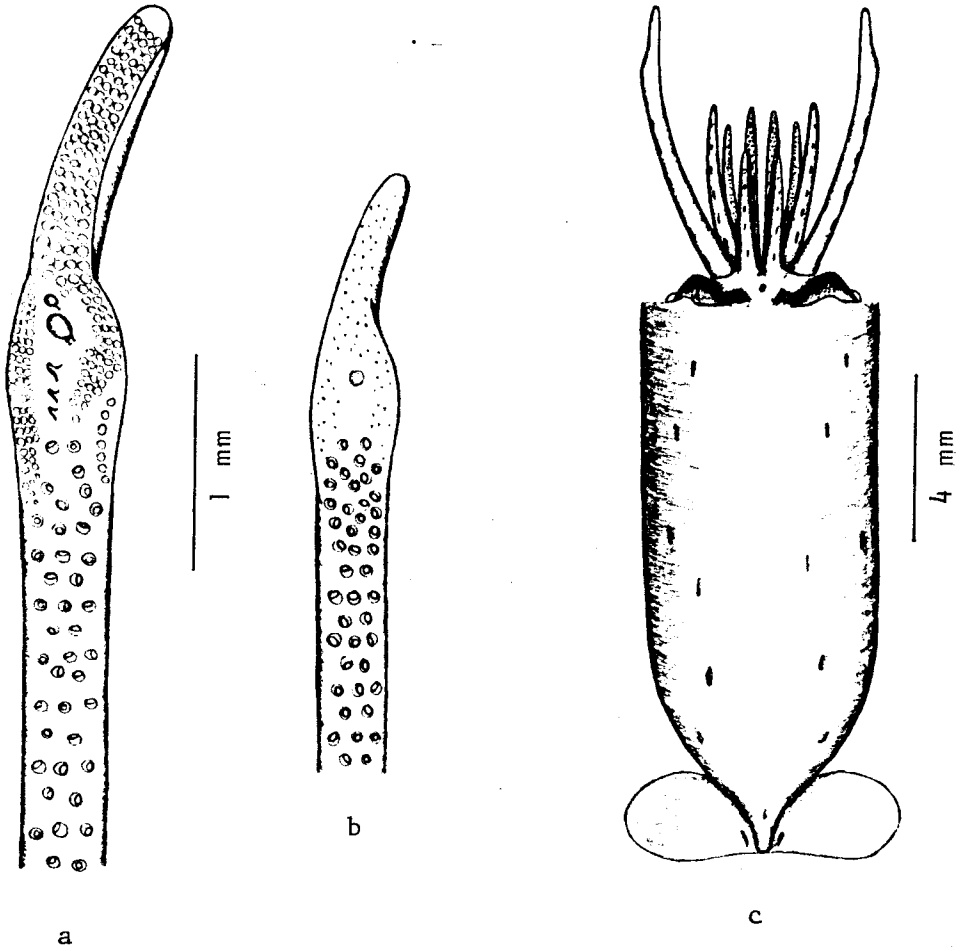

Plate 24. *Gonatus* sp., post-larval stage: (a) tentacle from a 13 mm DML specimen, (b) tentacle from an 11 mm DML specimen and (c) ventral view of a 13 mm DML specimen.

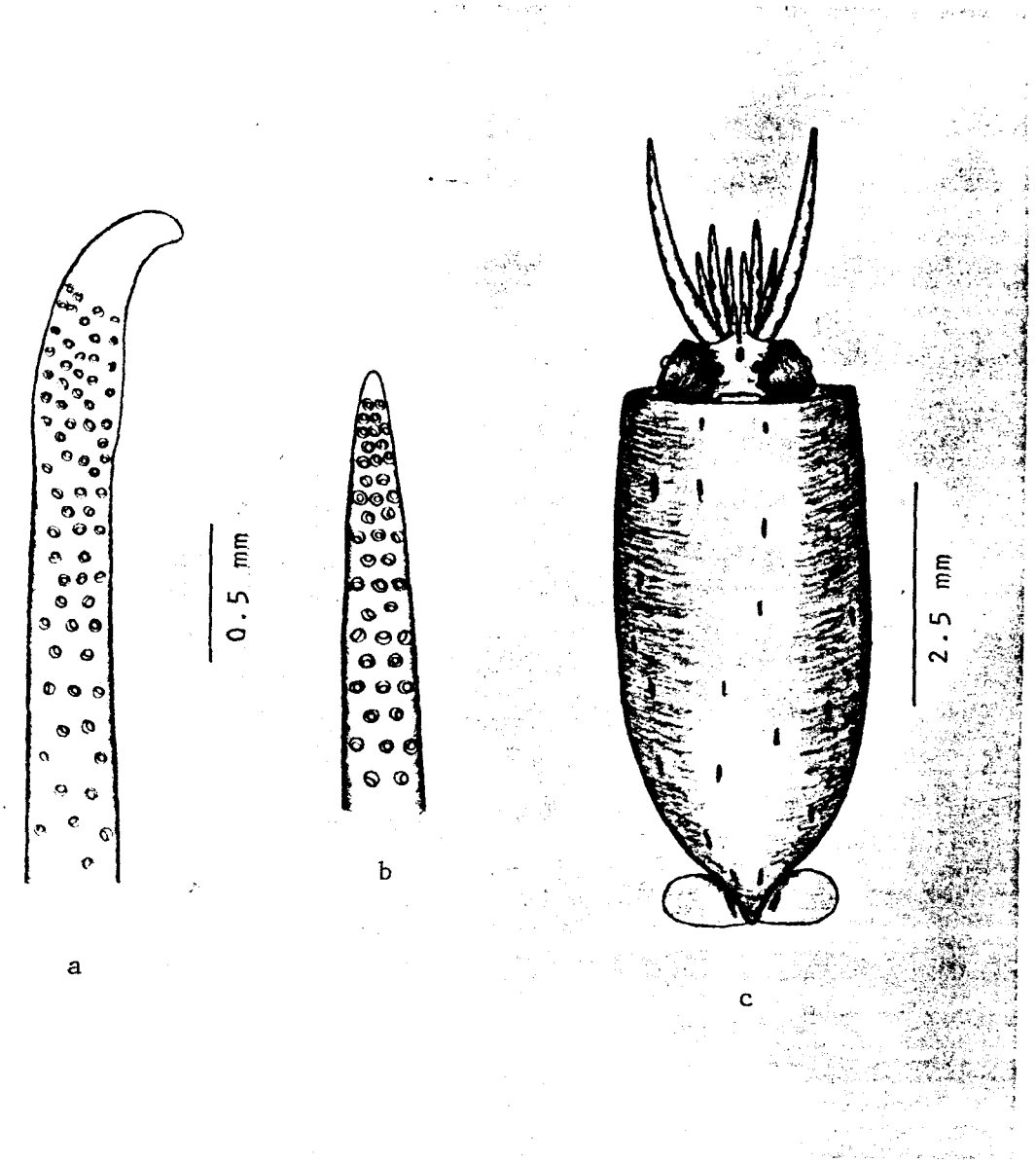

Plate 25. *Gonatus* sp., larval stage: (a) tentacle from a 9 mm DML specimen, (b) tentacle and (c) ventral view of a 6 mm specimen.

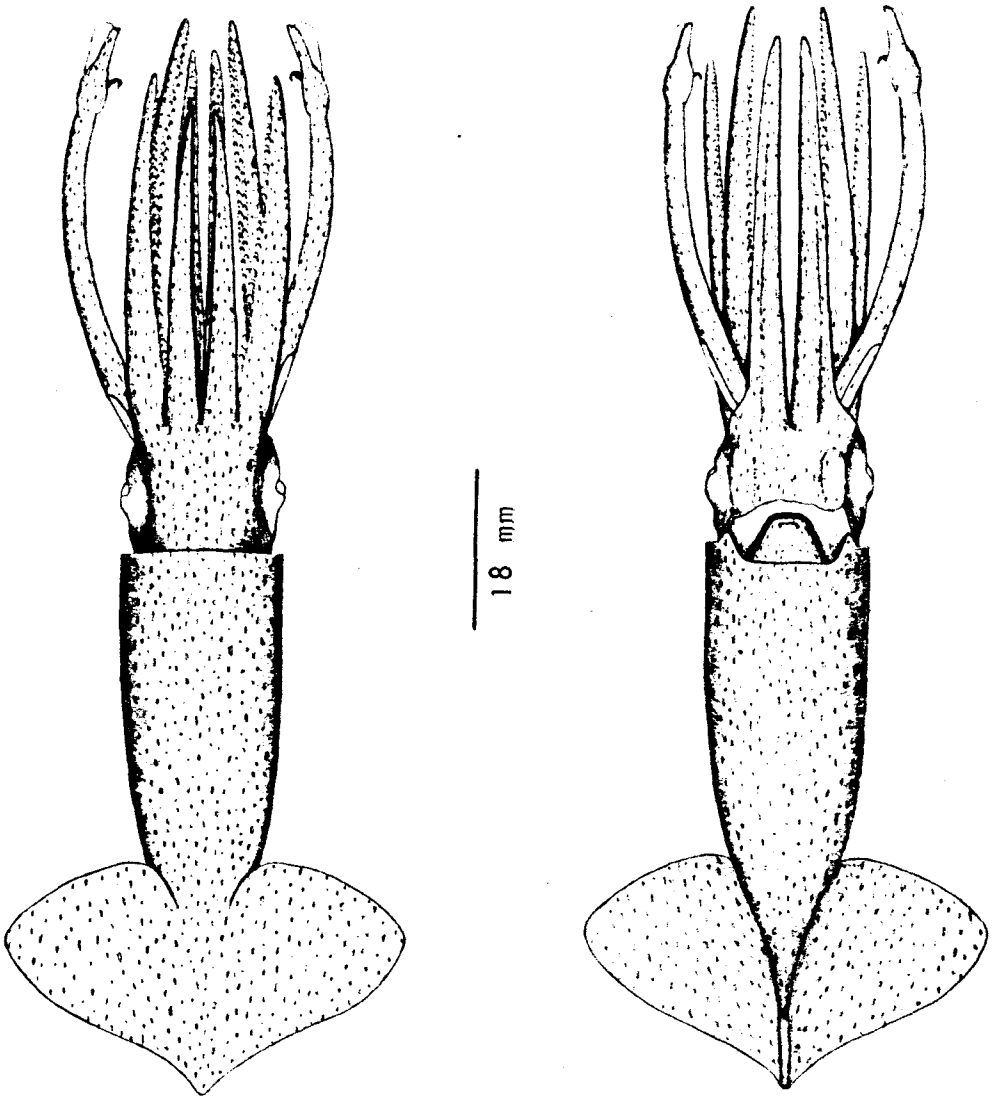

Plate 26. *Gonatus pyros*, adult stage: dorsal and ventral view of a 62 mm DML specimen.

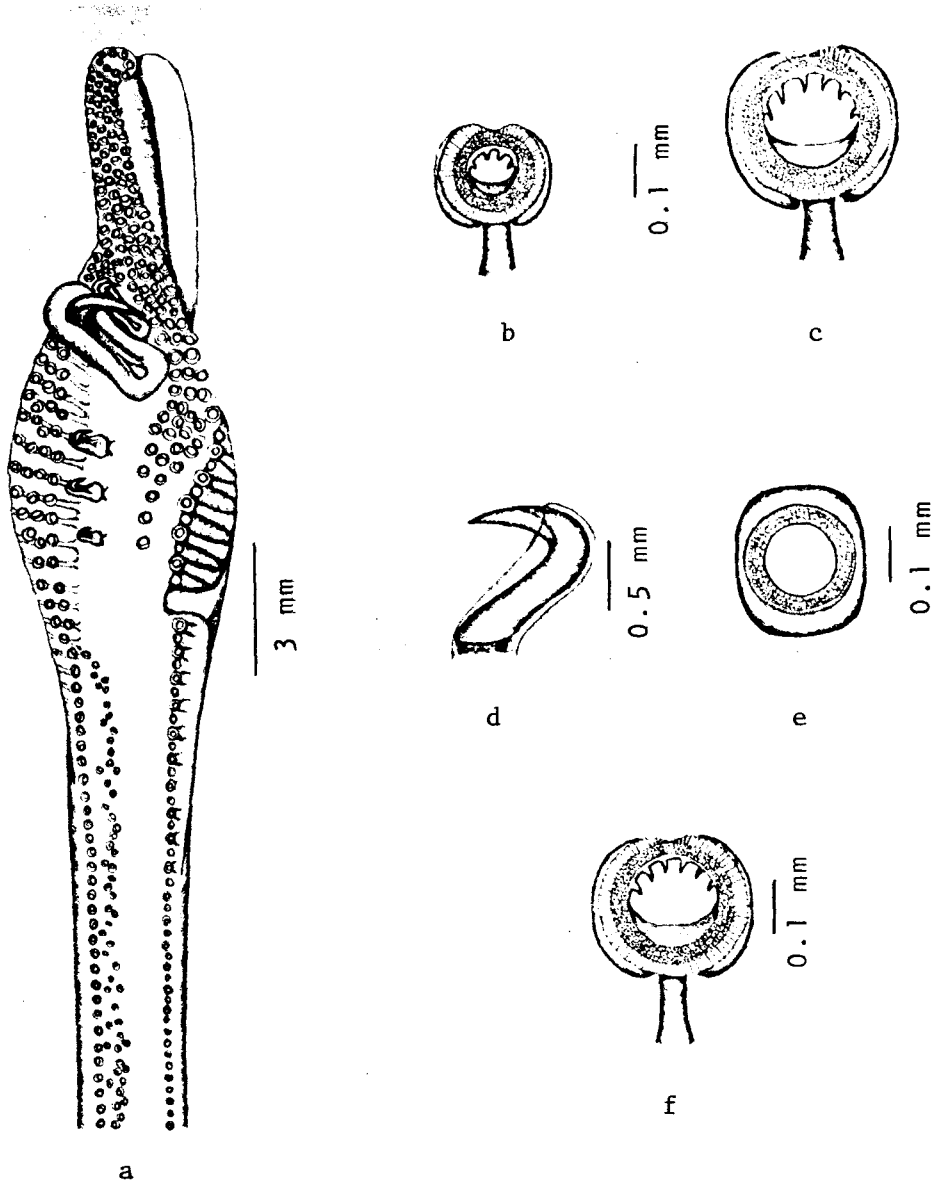

Plate 27. *Gonatus pyros*, adult stage: (a) tentacle from a 62 mm DML specimen, (b) largest sucker from the dactylus, (c) largest dorsal-marginal zone sucker, (d) largest proximal hook from the median zone, (e) largest locking zone sucker and (f) largest ventral-marginal zone sucker.

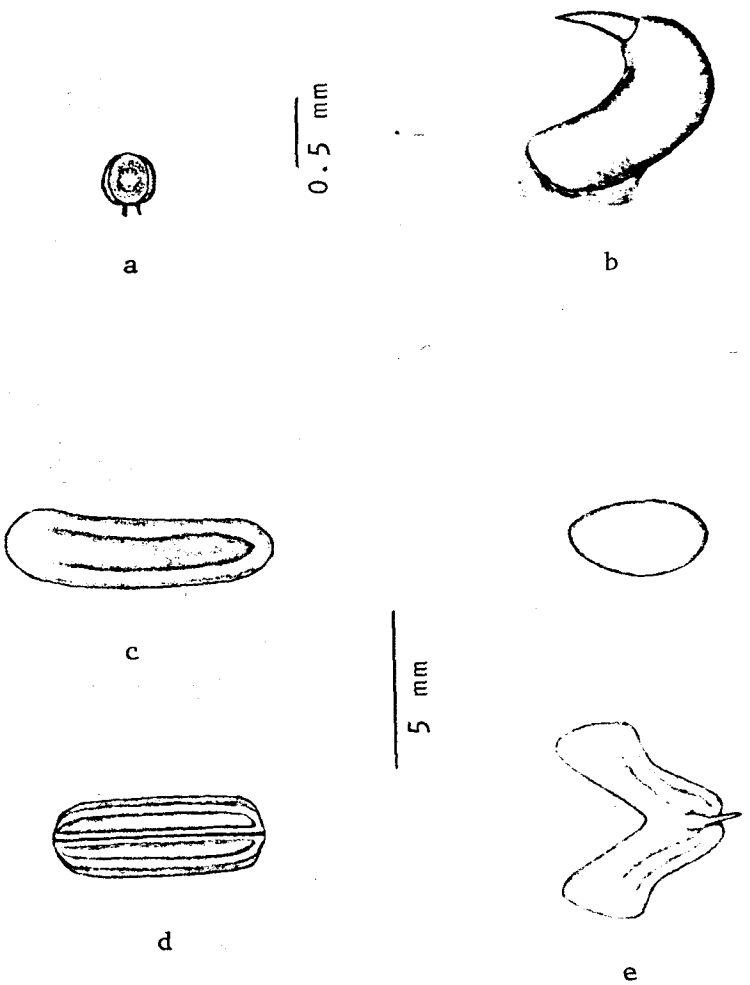

Plate 28. *Gonatus pyros*, adult stage: (a) largest lateral sucker from arm II, (b) largest median hook from arm II, (c) funnel locking cartilage, (d) nuchal cartilage and (e) funnel organ.

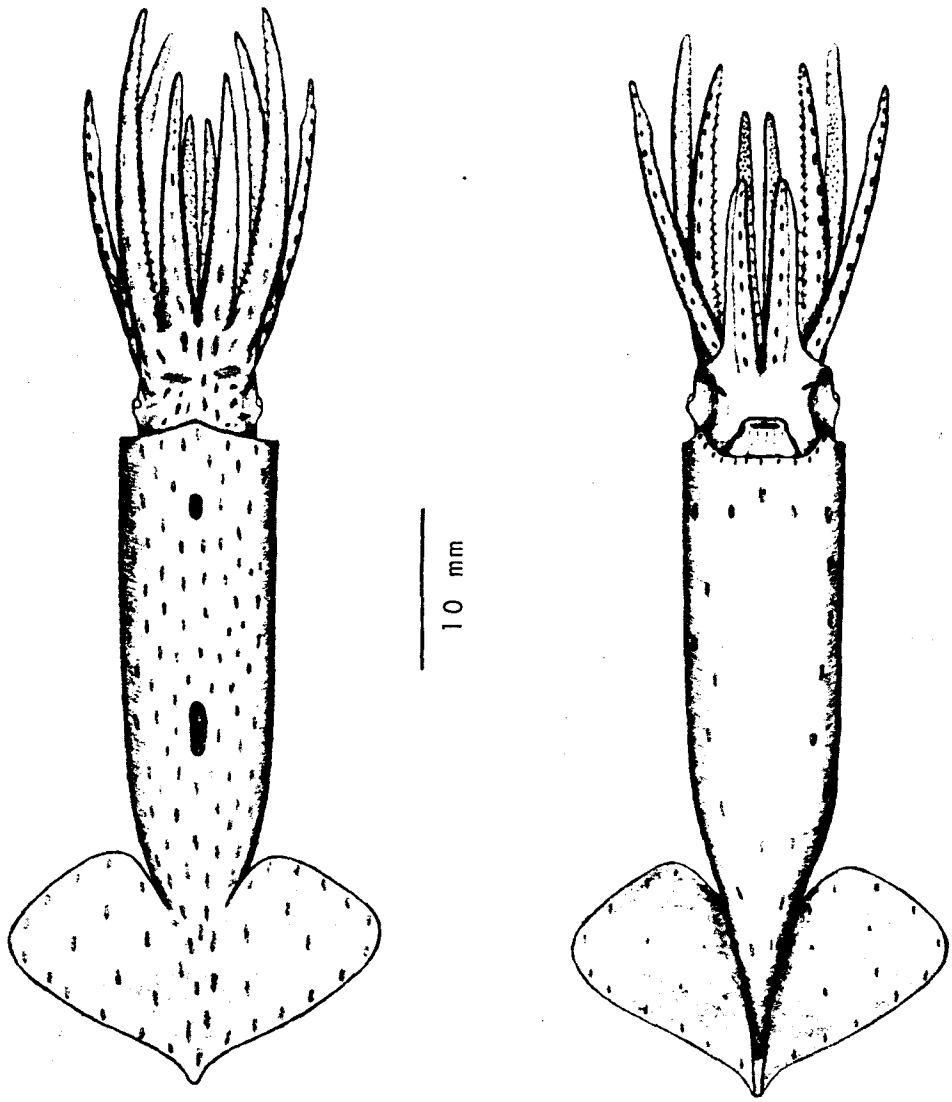

Plate 29. *Gonatus* type A, adolescent stage: dorsal and ventral view of a 44 mm DML specimen.

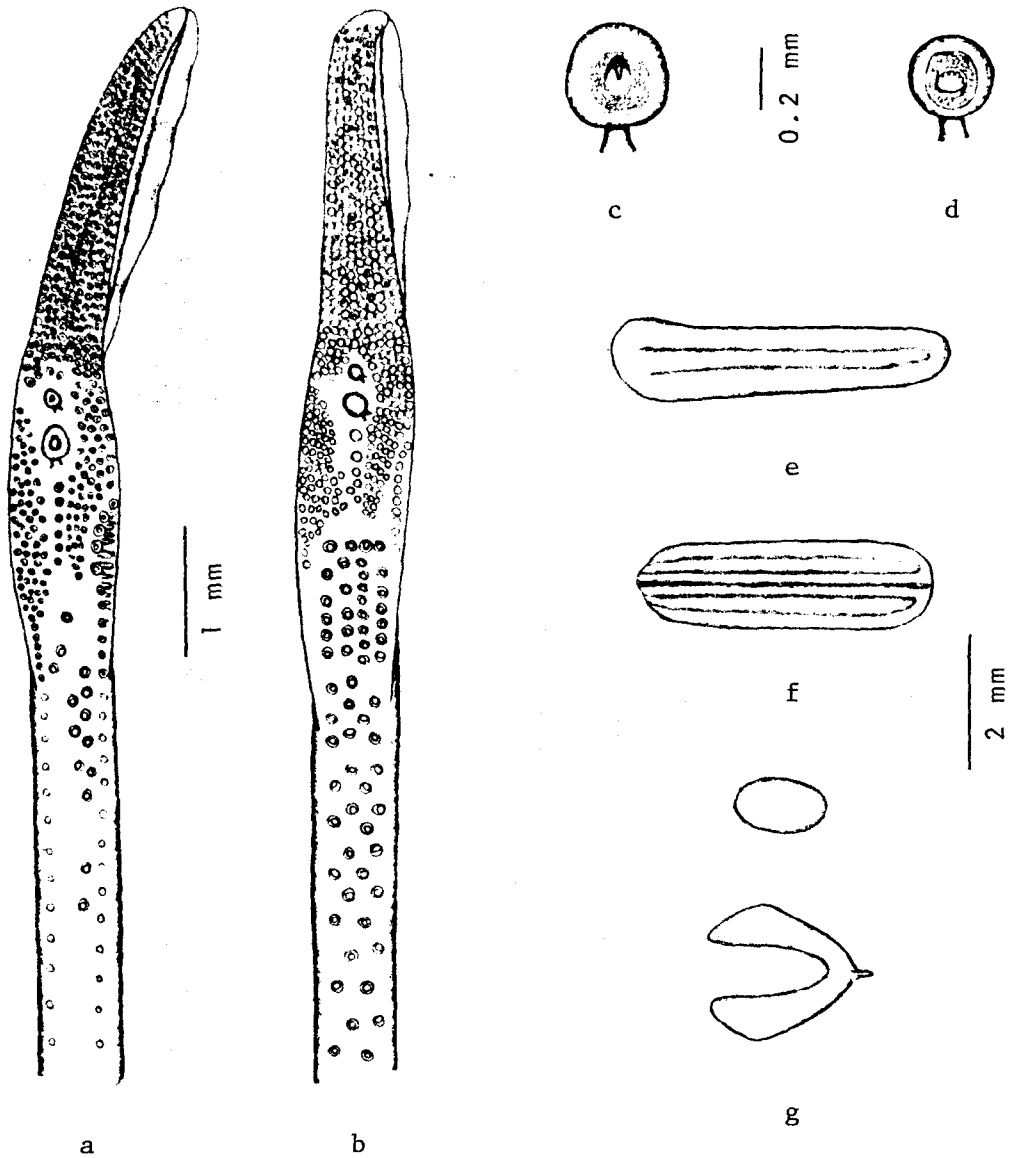

Plate 30. *Gonatus* type A, adolescent stage: (a) tentacle from a 44 mm DML specimen, (b) tentacle from a 38 mm DML specimen (c) largest median metamorphosing hook from arm III, (d) largest lateral sucker, (e) funnel locking cartilage, (f) nuchal cartilage and (f) funnel organ from a 44 mm DML specimen.

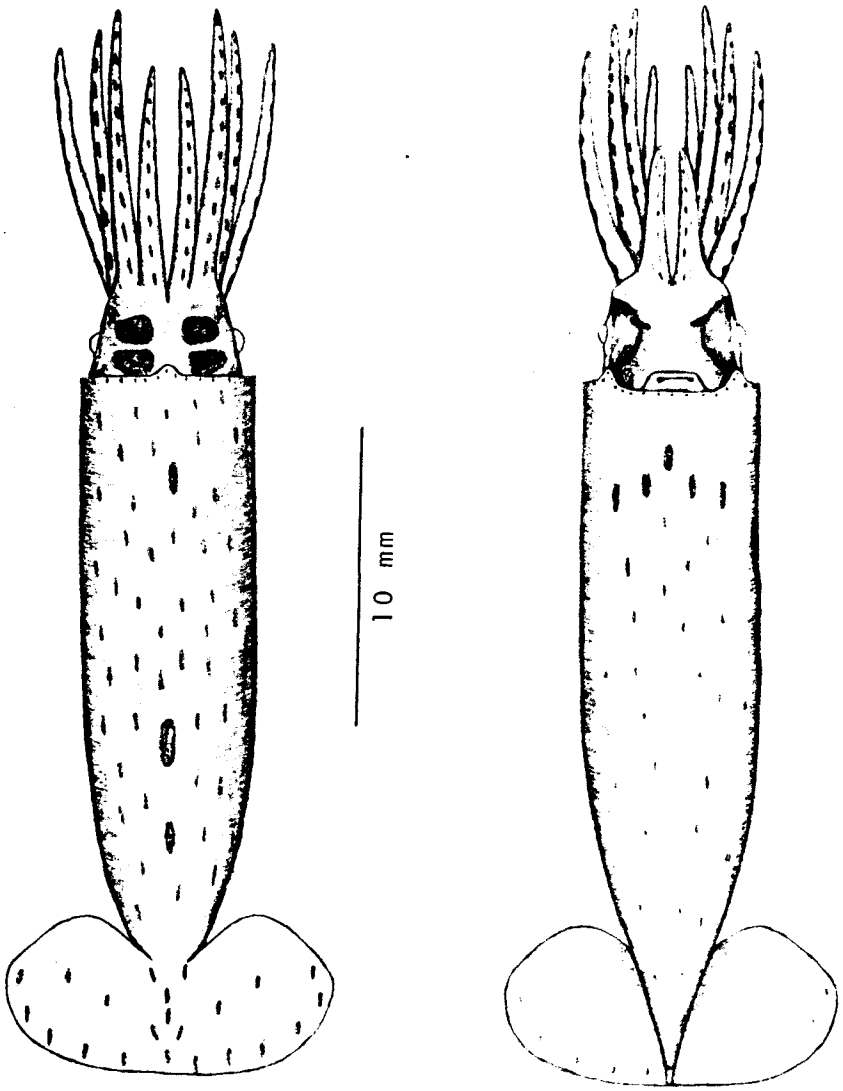

Plate 31. *Gonatus* type A, post-larval stage; dorsal and ventral view of a 25 mm DML specimen.

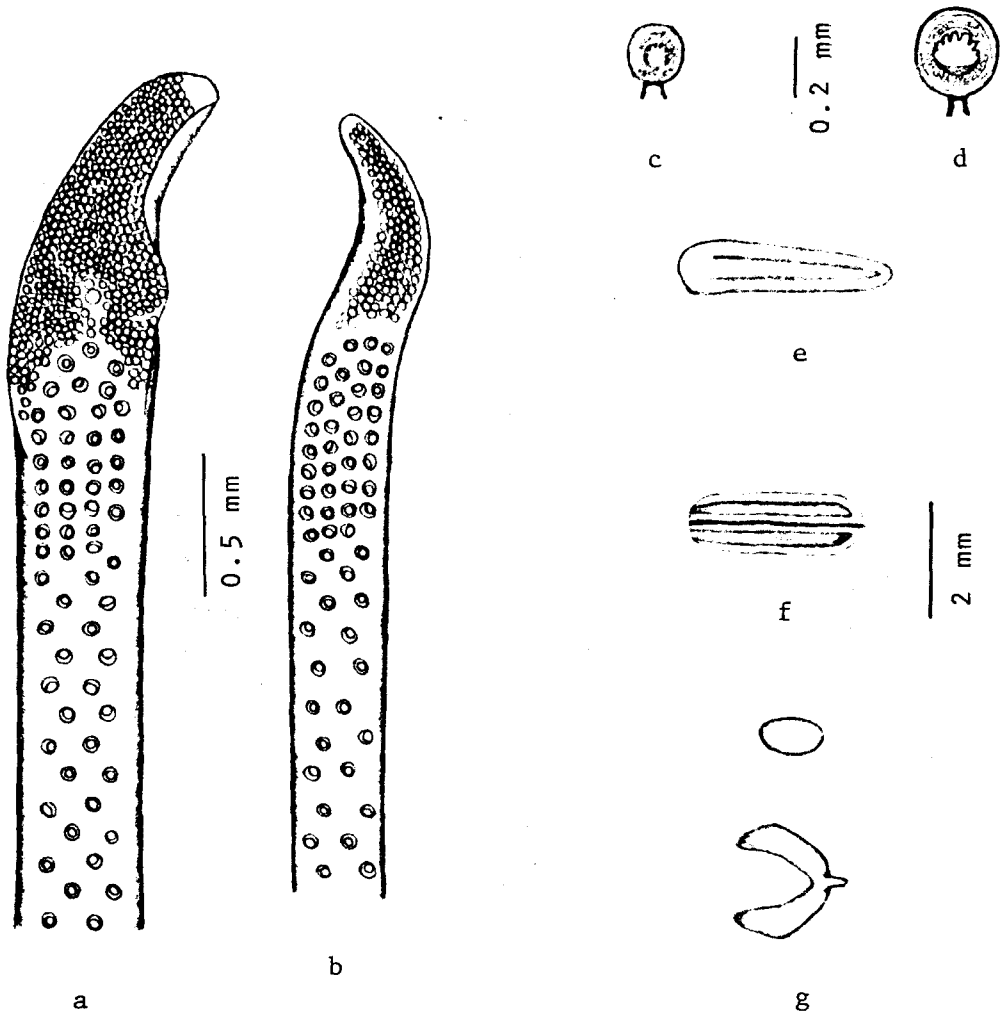

Plate 32. *Gonatus* type A, post larval stage: (a) tentacle from a 25 mm DML specimen, (b) tentacle from a 17 mm DML specimen, (c) median sucker from arm II, (d) corresponding lateral sucker from arm II, (e) funnel locking cartilage, (f) nuchal cartilage and (g) funnel organ from a 25 mm DML specimen.

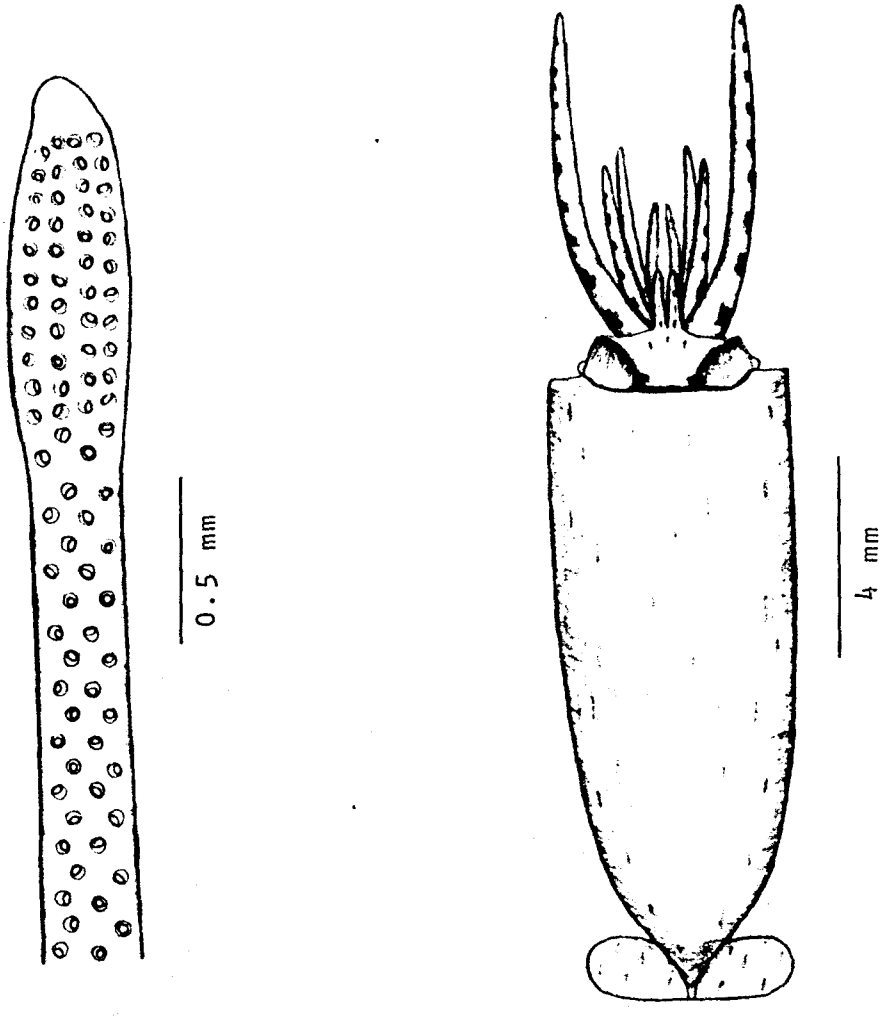

Plate 33. *Gonatus* type A, larval stage: (a) tentacle and (b) ventral view of a 12 mm DML specimen.

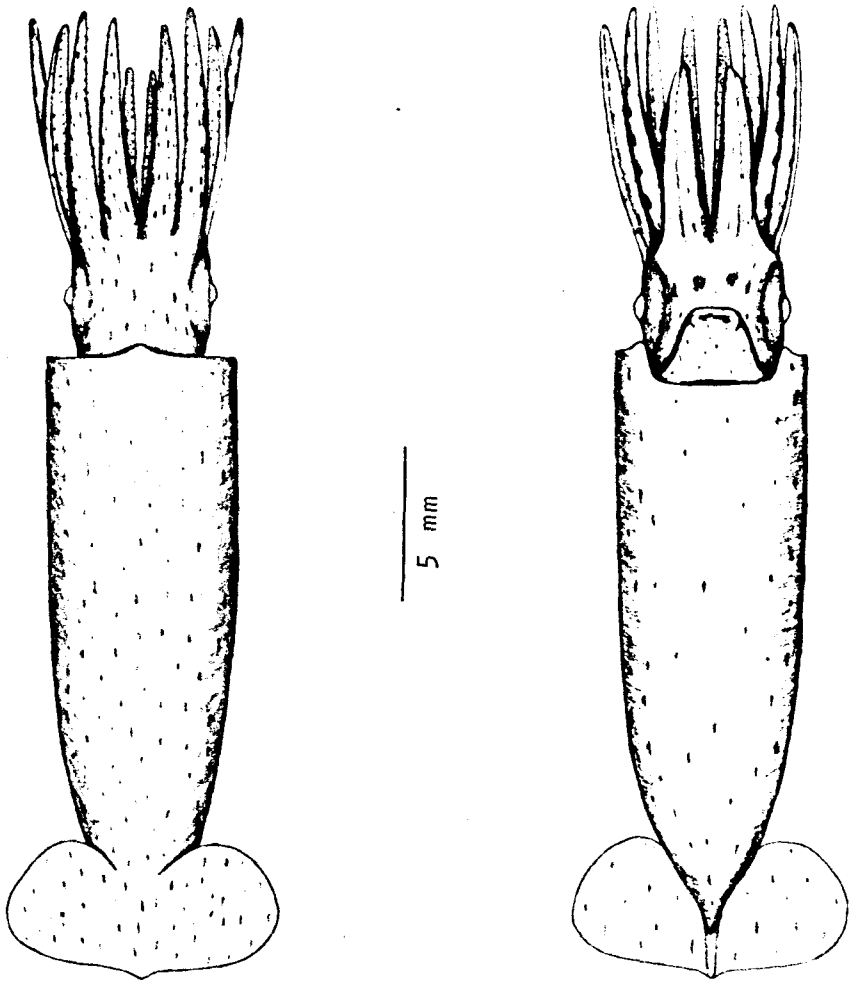

Plate 34. *Berryteuthis anonychus*, adolescent stage: dorsal and ventral view of a 23 mm DML specimen.

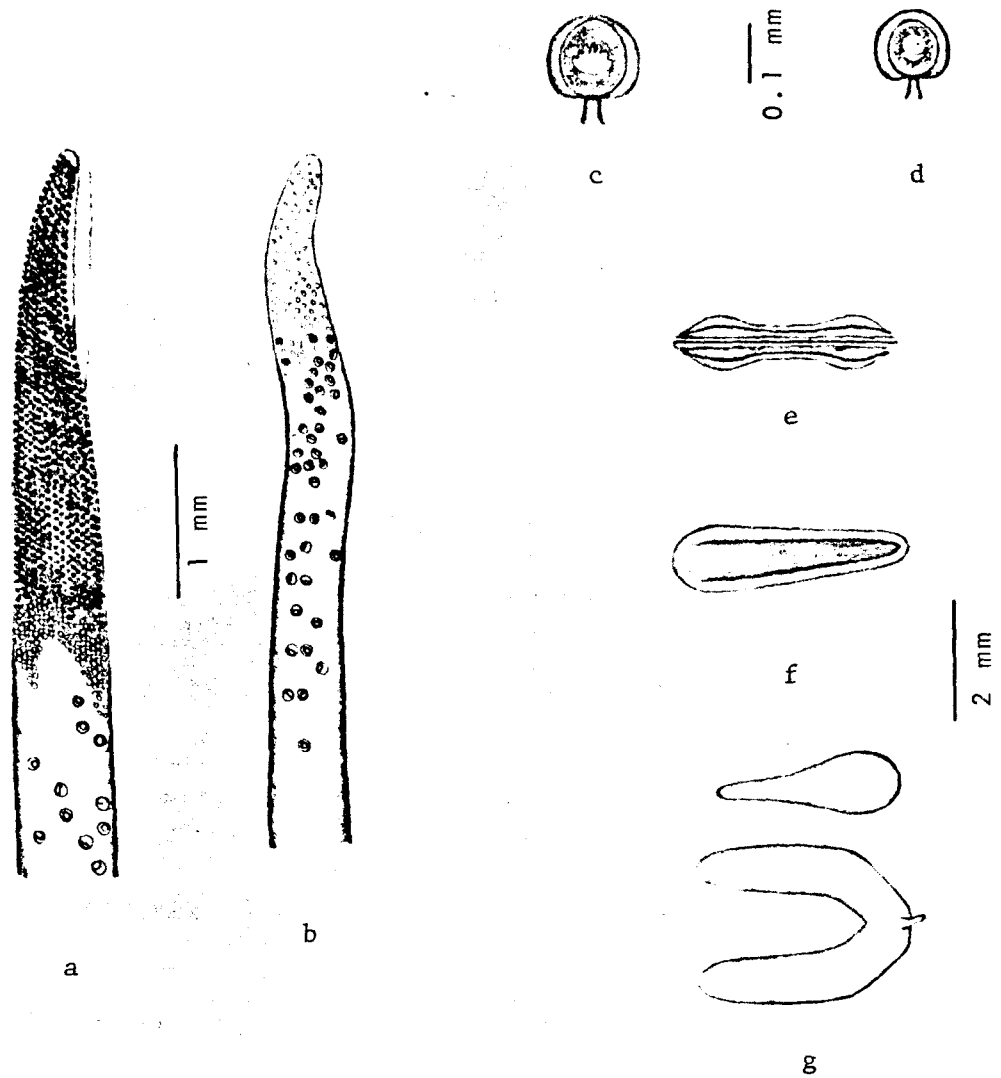

Plate 35. *Berryteuthis anonychus*, adolescent stage: (a) tentacle from a 23 mm DML specimen, (b) tentacle from a 14 mm DML specimen, (c) largest lateral sucker from arms II, (d) largest median sucker from arms II, (e) nuchal cartilage, (f) funnel locking cartilage and (g) funnel organ of a 23 mm DML specimen.

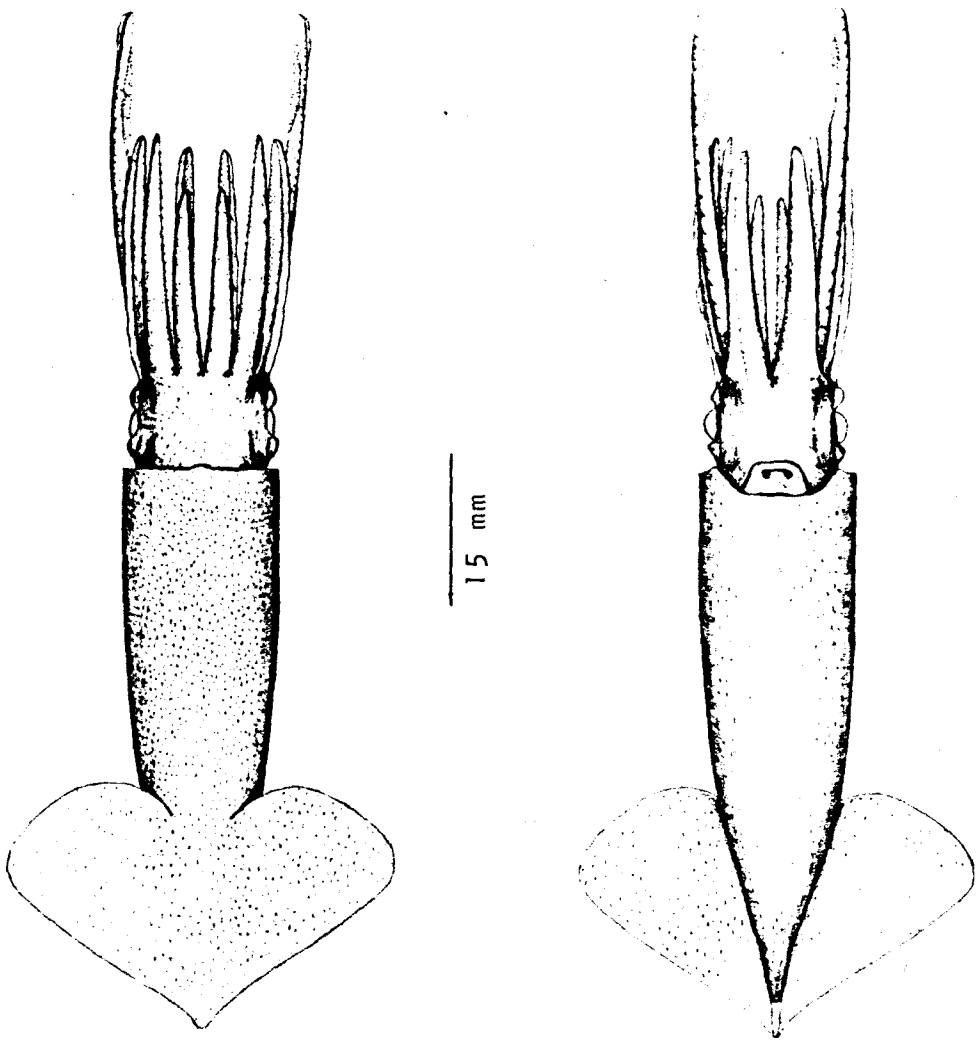

Plate 36. *Berryteuthis magister*, adult stage: dorsal and ventral view of a 57 mm DML specimen.

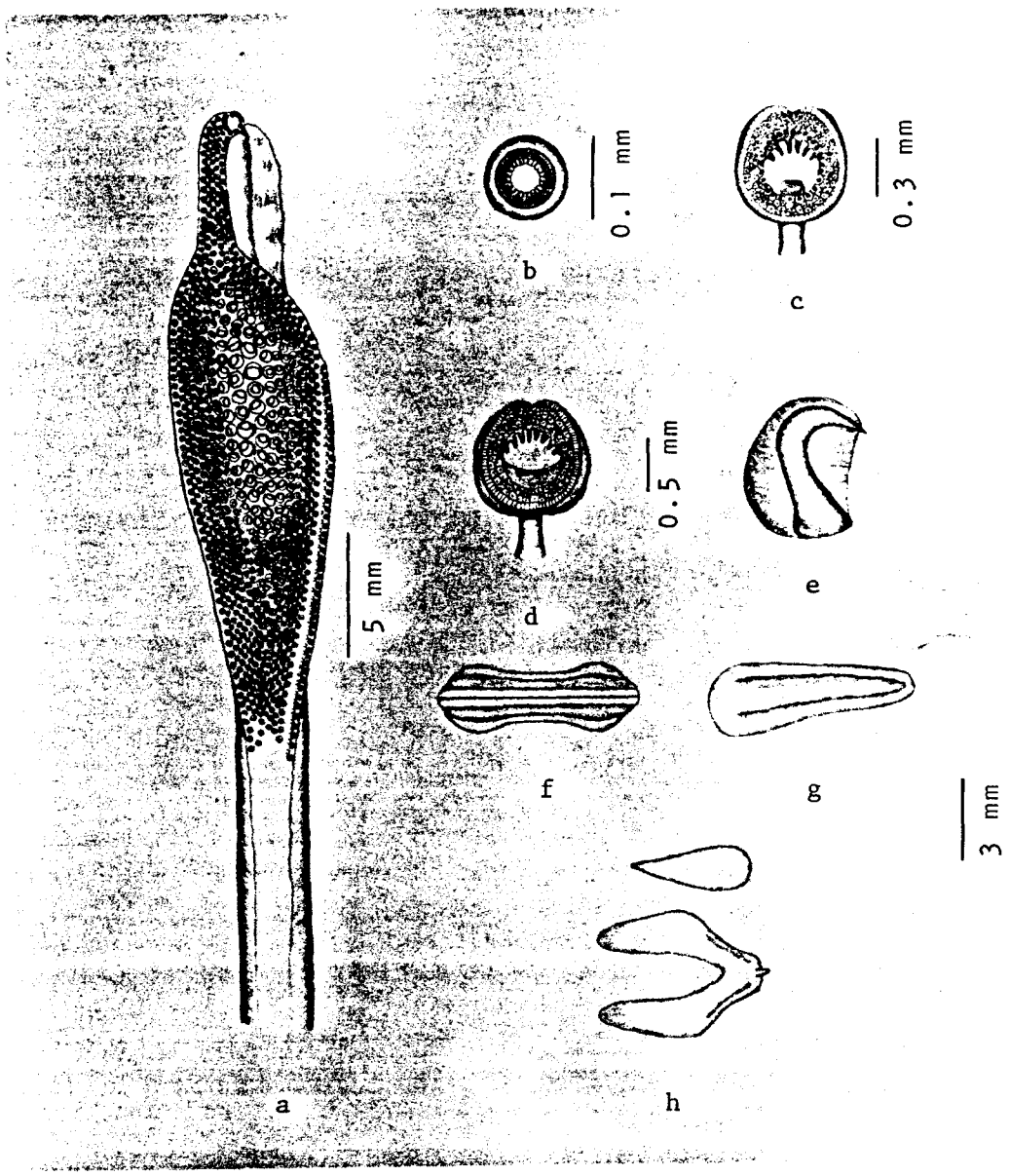

Plate 37. *Berryteuthis magister*, adult stage: (a) tentacle, (b) sucker from fixing apparatus, (c) largest sucker from manus, (d) largest lateral sucker from arms II, (d) largest median hook from arms II, (f) nuchal cartilage, (g) funnel locking cartilage and (h) funnel organ from a 57 mm DML specimen.

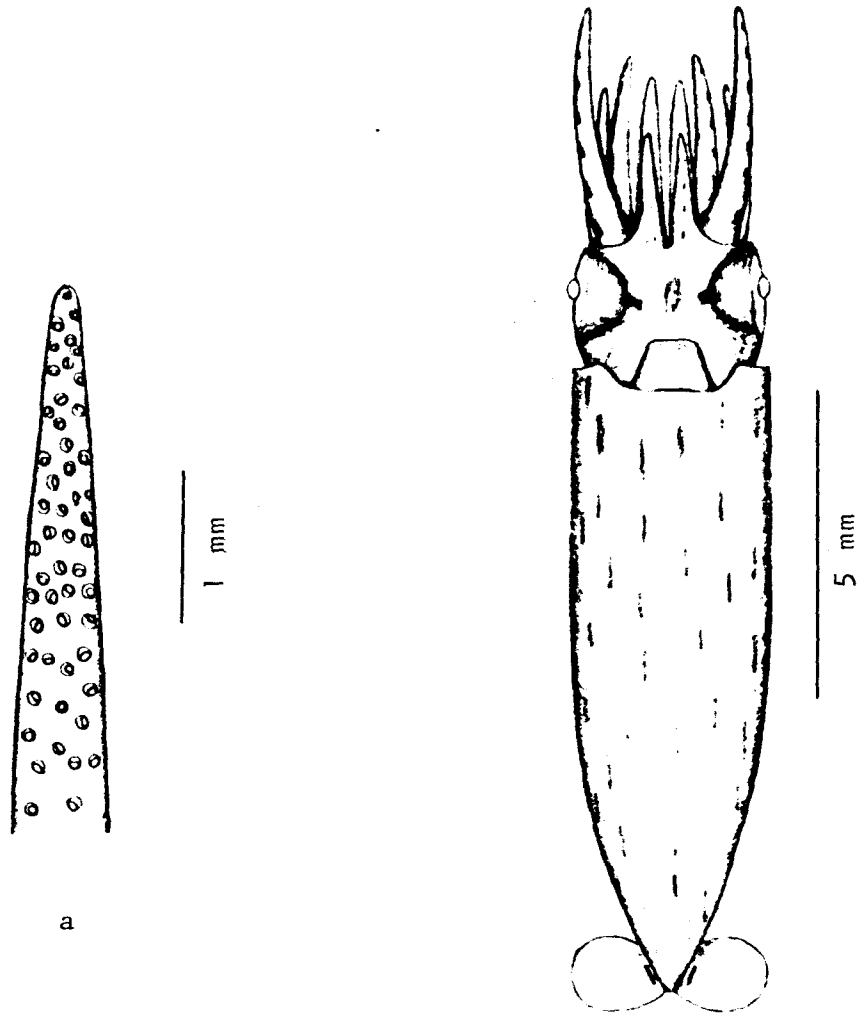

Plate 38. *Berryteuthis* sp., larval stage: (a) tentacle and (b) ventral view of a 9.3 mm DML specimen.

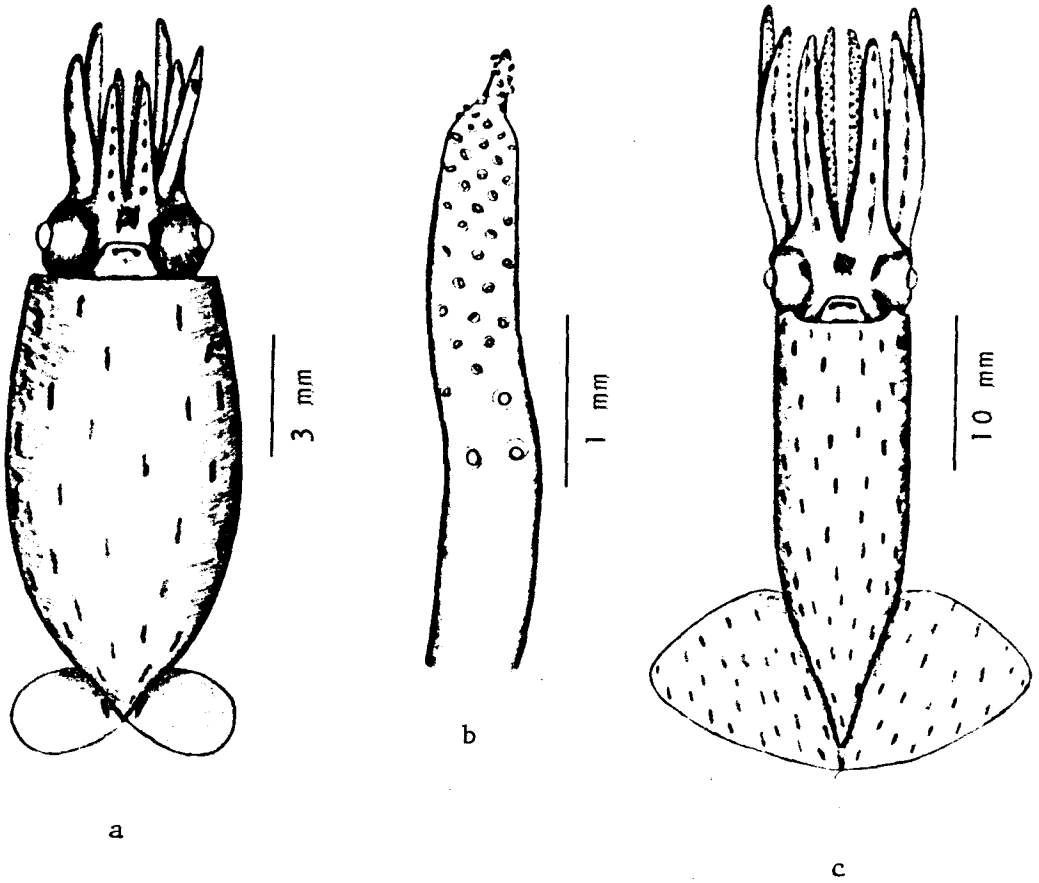

Plate 39. *Gonatopsis borealis*: (a) ventral view and (b) tentacle of a 9 mm DML post-larval specimen and (c) ventral view of a 31 mm DML adolescent specimen.

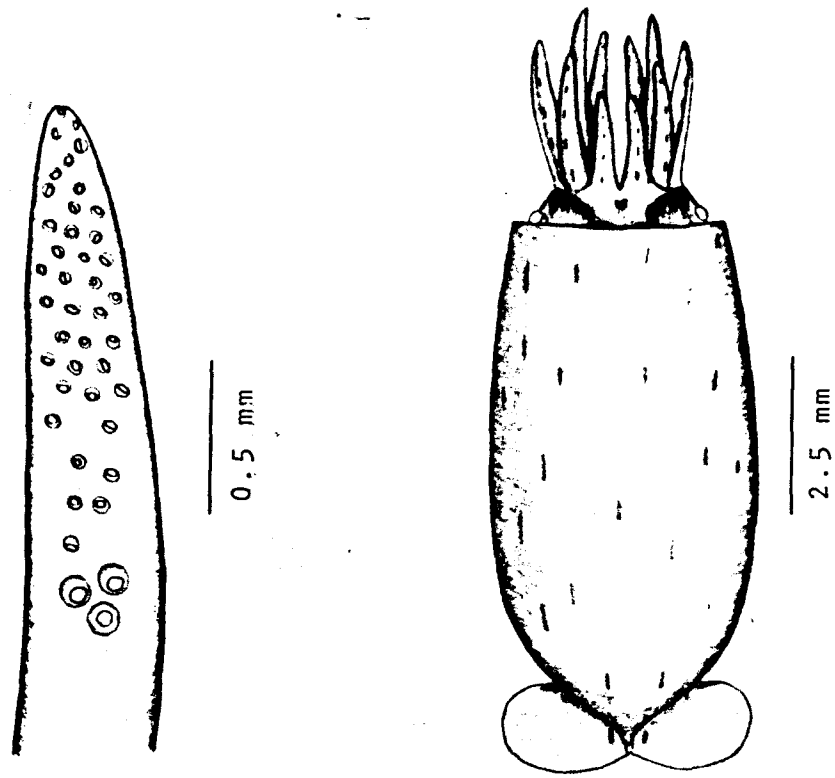

Plate 40. *Gonatopsis borealis*, larval stage: (a) tentacle and (b) ventral view of a 8 mm DML specimen.

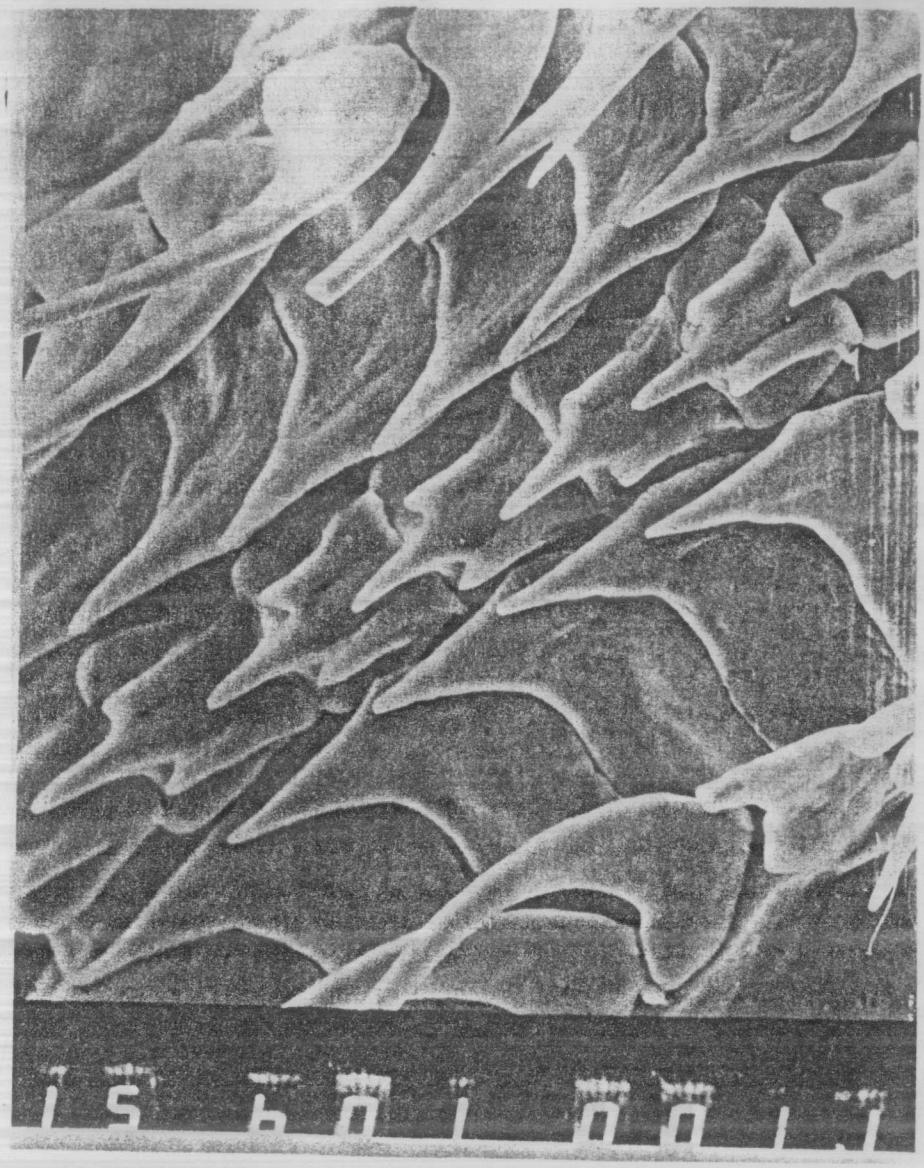

Plate 41. *Gonatus tinro*, radula of a 16 mm DML specimen.

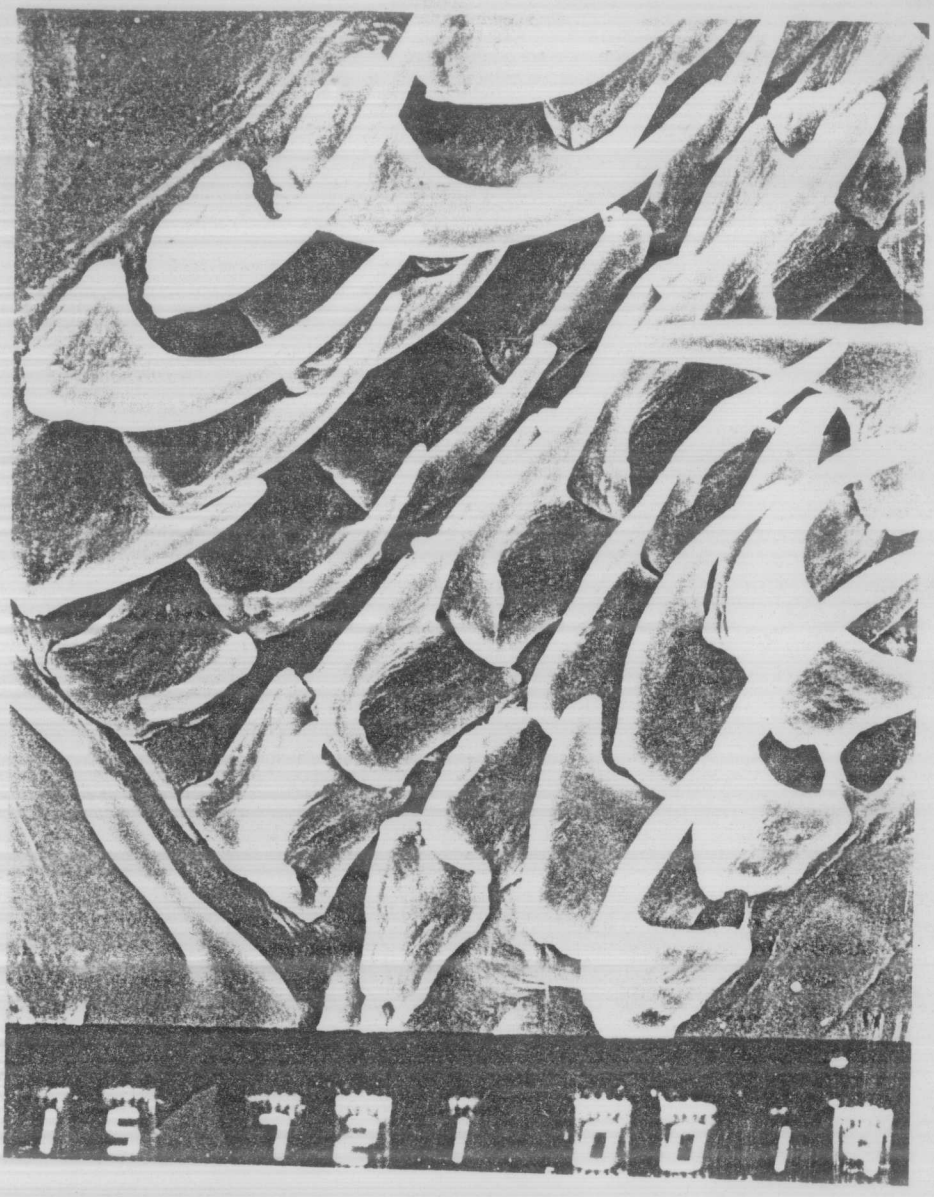

Plate 42. *Berryteuthis anonychus*, radula of a 16 mm DML specimen.