"Larval" and Juvenile Cephalopods: A Manual for Their Identification

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ABSTRACT

Sweeney, Michael J., Clyde F.E. Roper, Katharina M. Mangold, Malcolm R. Clarke, and Sigurd v. Boletzky, editors. "Larval" and Juvenile Cephalopods: A Manual for Their Identification. *Smithsonian Contributions to Zoology,* number 513, 282 pages, 277 figures, 6 tables, 1992. This manual provides a practical guide to the identification of "larval" and juvenile cephalopods. A comprehensive glossary of morphological terms is presented, as is a general pictorial key to the young stages of cephalopods, primarily to the family level. Systematically organized by order and family, the manual presents characters for adult and young forms, keys, illustrations, distributional and biological information, and references to pertinent literature.

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Contents

This volume is dedicated with gratitude and honor to Professor Gilbert L. Voss (1918–1989), a leading figure in cephalopod systematics and biology for nearly 40 years. In the early 1950s Dr. Voss intended to conduct research on larval and juvenile cephalopods of the Florida Current, but he was forced to abandon the project because even the adults from the Gulf of Mexico and the Caribbean Sea were mostly unknown. This was a world-wide problem and only by the mid 1980s was faunal knowledge sufficiently improved to attempt a compilation about larval cephalopods on a world-wide basis. This volume, in no small part, represents the tremendous contributions Gil Voss has made to cephalopod systematics and distribution.

Preface

This manual results from an intensive international workshop and subsequent efforts by most participants. The following summary (adapted from Roper, 1985:94, 95) provides readers with the historical perspective and organizational context from which this collaborative volume emerged.

The concept of establishing an international body of cephalopod specialists to assess and encourage the direction and needs of cephalopod research was introduced and accepted at the International Workshop on the Biology and Resource Potential of Cephalopods, held in Melbourne, Australia, in March 1981. Shortly thereafter, during the workshop on cephalopod beaks from predator stomachs, which was held at the Marine Biological Laboratory, Plymouth, England, in June 1981, the charter members of the new organization convened a working group to develop the organizational structure for the Cephalopod International Advisory Council (CIAC). The Charter Committee then met at Laboratoire Arago, Banyuls-sur-Mer, France, in September 1983 to formally accept the charter and resolutions and to elect the first regular council members. The membership of CIAC consists of 18 internationally recognized scientists who specialize in research on cephalopods. Membership is on a rotating basis in order to maintain stability and direction and at the same time to provide opportunity for participation from as broad a spectrum of cephalopod research interests and geographical representation as possible. The objectives of CIAC are (1) to stimulate and to influence scholarly research on cephalopods from an international perspective, (2) to provide information, advice, and assistance on all aspects of cephalopod biology, including those associated with the development and management of cephalopod fisheries resources, and (3) to disseminate information on past and current cephalopod research. To achieve these objectives CIAC will monitor and review the current status of research on cephalopods on a worldwide basis to provide an overview of results, directions, trends, needs, and problems. This will be accomplished through organization and sponsorship of international workshops, symposia, and training courses; production of handbooks, computerized cross-indexed bibliographies, review papers, and a periodic newsletter on living cephalopods; maintenance of a list of experts available as consultants to any individual, organization, or government requiring information, advice, and assistance on any aspect of cephalopod biology and fisheries.

The Cephalopod International Advisory Council is affiliated with the International Council of Scientific Union's International Association of Biological Oceanography (IABO), sponsored through UNESCO. Further, the CIAC charter provides for a representative of the Food and Agriculture Organization of the United Nations to serve as a permanent observer on the Council.

The establishment of CIAC by working scientists as a recognized international organization has enabled the rapid implementation of objectives. For example, as a result of a written survey of many cephalopod scientists from around the world, CIAC concluded that the single most urgent problem facing cephalopod researchers is the inability to identify "larval" and early juvenile stages of cephalopods. Here was a clearly recognized need to which CIAC was able to respond by organizing and sponsoring an international workshop and symposium held in June 1985, at Laboratoire Arago, Banyuls-sur-Mer, France. The results of the symposium have been published in a special volume: Mangold, K. and S. v. Boletzky, editors, 1985. The Biology and Distribution of Early Juvenile Cephalopods. *Vie et Milieu*, 35:137-302.

Since the beginning of studies on cephalopods, the identification of virtually all stages of young and juvenile forms has been confusing and problematic; the inability to identify the young stages has created a serious impediment to progress of research in cephalopod ecology, systematics, and fisheries. This is especially the case for species that constitute

the huge biomass upon which the major fisheries are based, and includes the numerous species of *Loligo*, the adults of which provide the giant nerve axons used in biomedical research. In recognition of the urgent need for new perspectives of identification, the workshop included scientists from a variety of diciplines such as comparative morphology, systematics, and behavior.

The specific aims of the workshop were to (1) develop and refine standardized methods of identifying "larval" and early juvenile growth stages of cephalopods to the generic or species level, (2) report current research on various aspects of biology of early growth stages of cephalopods, especially concerning identification, distribution, abundance, ecology, behavior, and prey-predator relationships, (3) formulate future research directions based upon a worldwide view of cephalopod resources available for basic and applied research, (4) discuss future workshops and collaborative programs based upon needs and views of the workshop participants, and (5) publish a handbook resulting from the findings of the workshop.

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EDITORS

Introduction

This manual represents the product of a workshop organized by the Cephalopod International Advisory Council (CIAC) held at Laboratoire Arago, Banyuls-sur-Mer, France, 17–28 June 1985. During the workshop 35 participants (see Appendix) from 11 countries examined a large collection of young cephalopods brought from all seas and oceans in order to assemble and advance our knowledge of "larval" and juvenile forms. The activity at the workshop and subsequent work by participants on the literature and additional specimens have resulted in this publication, which represents the present state of knowledge on the taxonomy of young cephalopods. The extent that advances in knowledge proved possible depended upon the amount of material available to the workshop participants and varied from family to family. Young forms are still not known for many species and for some entire families; in such cases the adult features are described so that when material becomes available, young forms may be recognized by tracing characters from larger to smaller individuals. Previously, few detailed studies have been made relating "larvae" to adults. The assembly of information below is meant to aid and stimulate future work as well as provide a reliable source in itself.

One of the early controversies that arose at the workshop concerned the validity and usefulness of the term "larva." As a result, the problem was examined in detail by Young and Harman (1988). They concluded that a valid argument can be made for the use of the term if the precedent set by fish terminology is accepted. However, when applied to cephalopods in general, the term "larva" would necessitate the broadening of an already abused concept and would be operationally undefinable. They proposed a new term "paralarva" for the planktonic young of cephalopods that meet certain ecological, and in some cases, morphological criteria. Because "paralarva" is based, at least partially, on ecological criteria, it would not compete with the developmental terms "larva" or "juvenile." Technically, a young cephalopod can be both a larva and a paralarva, or a juvenile and a paralarva. The term, as presented, fills a clear need in our present terminology.

Young and Harman (1988:202) defined paralarva as "a cephalopod of the first post-hatching growth stage that is pelagic in near-surface waters during the day and that has a distinctly different mode-of-life from that of older conspecific individuals." These authors also redefined "juvenile" as the developmental stage between hatching and the subadult stage, or if "larva" is applied as the post-hatching developmental stage in certain groups (e.g., Cranchiidae), the "juvenile" is defined as the stage between the larval and subadult stages. In the latter case, the criteria that separate these stages are undefined. The term "subadult" defines the stage between the juvenile and the adult stages. The subadult stage commences with the full attainment of morphological features used to define the species other than those relating to size and sex, and terminates with the attainment of sexual maturity.

This terminology was not available at the time manuscripts were written for the present manual. As a result, contributors have used terms of their choice.

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This paper was reviewed by Dr. Robert Robertson, Department of Malacology, Academy of Natural Sciences of Philadelphia.

Although each family has been compiled largely by the author(s) listed, other workshop participants frequently were involved (see Appendix 2); a few workers who had special knowledge but were unable to attend the workshop (e.g., Dr. T. Okutani) were consulted afterward, and the editors are particularly grateful for their help.

Spawn and mature eggs are known for only a few neritic species and for an even fewer number of oceanic species. In cases where no references are made in the text, it can be assumed that the eggs are unknown.

In comparing very young forms it is desirable that the size is recorded at which the acquisition of adult features or the disappearance of "larval" features takes place. This is not always possible in rare species where size-graded series of specimens are not available. In many cases, we quote a size at which a feature is present or absent as a guide to the identification, but often further material is required to establish a more precise mantle length at which a change occurs. Thus, for example, if our smallest specimen is 30 mm in mantle length and we record a photophore at that length, we do not exclude the possibility that the organ actually will be recognizable at 10 mm mantle length.

Not all known species in some families are included in the text, because their young forms are undescribed. Investigators working on poorly studied faunas should be aware that these species may not be identifiable using this manual. Also, "group" is used with a taxon in a heading if there are probably multiple taxa involved.

The standard size of all cephalopods is expressed as the dorsal mantle length (ML) or occasionally as the gladius (pen) length (GL) in mm. In a few oceanic squids (e.g., Chiroteuthidae) the mantle is drawn out into a filiform extension containing little but the posterior portion of the gladius. In these forms mantle length is measured from the anterior mantle edge to the posterior level of the fins. In octopods, in which the dorsal mantle edge is not distinct, mantle length is taken from between the middle of the eyes to the posterior end of the mantle.

Although the literature cited is not comprehensive, it is sufficient to give anyone identifying young cephalopods a firm and expanded background for using the manual. We recommend consulting the literature quoted before publishing any identifications. Literature citations for each order or family can be found at the end of that section.

In this manual, each section (as defined by authorship) begins on a new recto page. This format is used to facilitate the creation of reprints by each group of authors.

The editors would be grateful for receiving corrections or additions to the manual from users if their knowledge or research can enhance the value of future editions. Copies of appropriate reprints or references concerning this information would be most appreciated.

All contributions to this volume have been subjected to critical review by a minimum of four specialists. Their criticisms, suggestions, and contributions are greatly appreciated.

ACKNOWLEDGMENTS.—The editors wish to express their warm thanks to everyone who worked to produce this handbook with a minimum of delay, especially the workshop participants and the specialists who were subsequently consulted. The great kindness and hospitality of the directors and staff of Laboratoire Arago at Banyuls-sur-Mer, France, during the workshop and compilation of the text is gratefully acknowledged. The lengthy typing of portions of the manuscript by J. Rembert is very much appreciated.

We are most appreciative of the financial support for the workshop extended by the Fisheries Resources and Environment Division, Food and Agriculture Organisation (FAO), Rome; the Programme Interdisciplinaire de Recherche en Oceanographie (PIROcean), Paris; and the Institut Francais de Recherche pour l'Exploitation de la Mer (IFREMER), Paris.

Glossary of Terms

(Adapted from Roper, Sweeney, and Nauen (1984) with inclusion of additional terms.)

Antitragus = A small knob-like cartilaginous projection from the posterior wall of the funnel locking-cartilage in some families (e.g., Chiroteuthidae, Mastigoteuthidae). See Tragus.

Arms = The eight circumoral appendages in adults of coleoid cephalopods. (One pair of modified appendages called "tentacles" lies between the ventral and ventrolateral arms in the "decapodous" Sepioidea and Teuthoidea; one pair of modified, greatly reduced appendages, called retractile filaments, lies between the dorsal and dorsolateral arms in Vampyromorpha.)

Arm crown = Inclusive term encompassing all circumoral appendages (arms, tentacles). See Circumoral appendages.

Arm-crown stalk = An elongation of the head between the eyes and the arm crown. Common in many "larval" and juvenile squids (e.g., Brachioteuthidae, Chiroteuthidae, Cranchiidae). Sometimes referred to as arm-crown pillar.

Band = Unbroken transverse line or series of chromatophores, may be simple or complex.

Bar = Short transverse line of chromatophores that represents broken or interrupted bands.

Buccal connectives = Muscular rods that connect the supports of the buccal membrane to the bases of the arms (Figure 1).

Buccal lappet = Small, subtriangular flap formed by the tip of the buccal membrane support and the adjoining buccal membrane; may bear suckers (Figure 1).

Buccal membrane = Thin web of tissue that encircles the mouth, reinforced by six to eight buccal supports (Figure 1).

Buccal membrane supports = Longitudinal muscular rods fused with the buccal membrane (Figure 1).

Buccal suckers = Small suckers on the buccal lappets/membrane (Figure 1).

Bullet-shape = Refers to posteriorly blunt, rounded, rather broad body (mantle) form common in "larval" cephalopods.

Calamus = The conical papilla or projection on the hectocotylus of octopods at the distal terminus of the sperm groove, distal to the last sucker and proximal to the ligula (Figure 2). See Ligula.

Calcified = Refers to incorporation of calcium carbonate in the organic matrix of shells of some Sepioidea (e.g., *Spirula, Sepia*). (All cephalopods have calcified statoliths in the statocysts.)

Carpal cluster (Carpal pad) = A usually distinct group of suckers and knobs on the carpus of the tentacular club (Figure 3).

Carpal knobs = Small, rounded, hemispherical protuberances on the carpus to which carpal suckers from the opposite club adhere during the locking of the clubs (Figure 3).

Carpal suckers = Small suckers on the carpus of the club that usually adhere to knobs on the opposite carpus during the locking of the clubs (Figure 3).

Carpus = The proximal zone of suckers and/or knobs on the tentacular club (Figure 3).

Cartilage (-inous) = A solid concentration of connective tissue-derived material occurring in funnnel-mantle locking apparatus, nuchal attachment, integumental "scales," cranium, etc.

Chitin = A mucopolysaccharide substance that forms the sucker rings, hooks, beaks, and gladii.

Chitinous = A generalized term for some hard structures in cephalopods that may contain chitin.

Chromatophore = Organs consisting of pigment-filled sacs with associated muscles and nerves that provide much of the background color, color patterns, and pattern changes of cephalopods.

Chromatophore, Extrategumental = The larval chromatophores located well beneath the integument.

Chromatophore fields = Suites of chromatophores that produce species-specific patterns in discrete regions of the body, namely arm, arm base, head, eye, mantle, viscera, and funnel.

Chromatophore, Tegumental = The chromatophores located in or near the surface integument.

Circumoral appendages = The eight arms (squids, cuttlefishes, and octopuses) and two tentacles (squids and cuttlefishes) or the very numerous tentacles (*Nautilus*) that arise from the head and encircle the mouth of cephalopods (Figure 1).

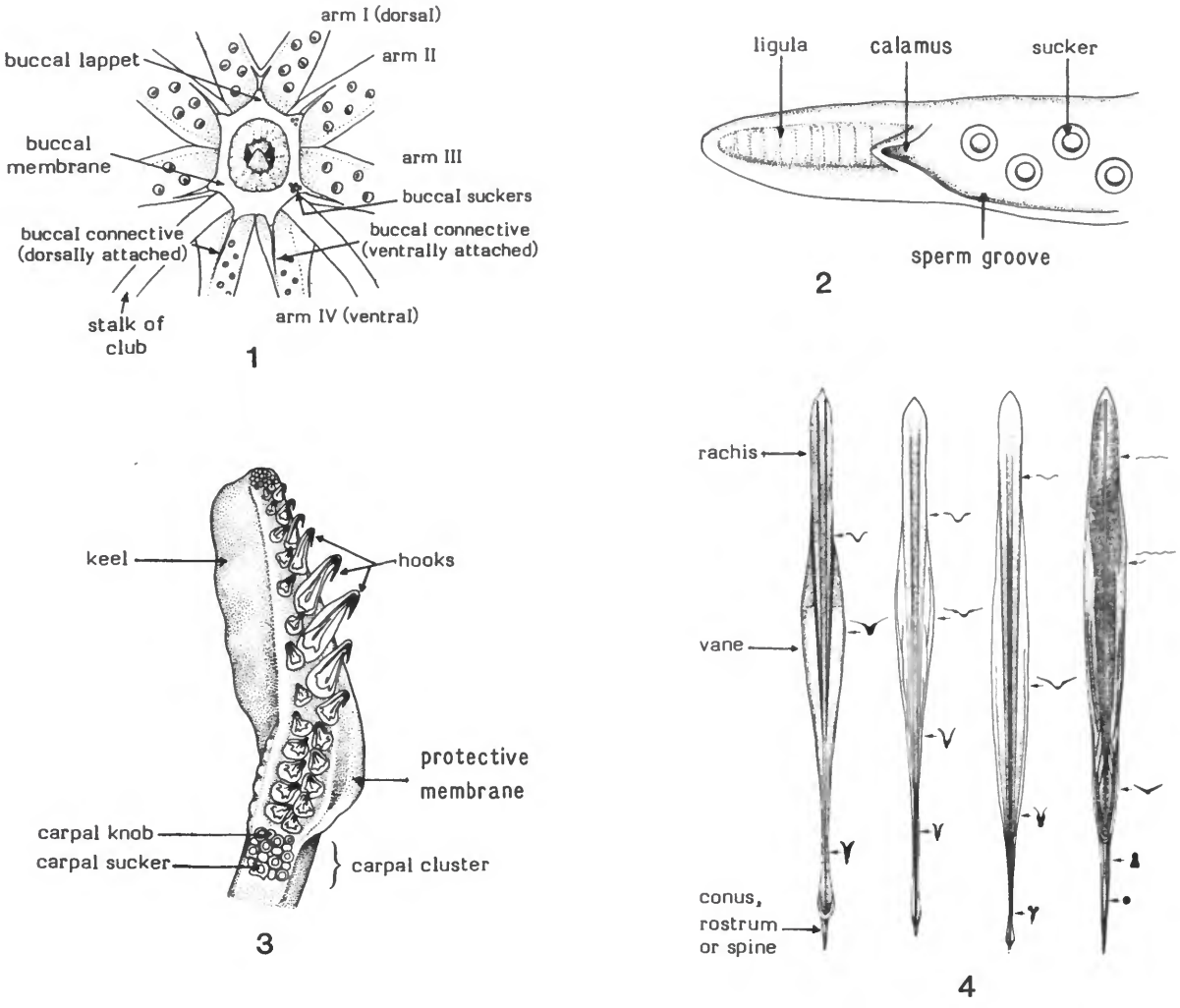
Cirri = Arm: Elongate, fleshy tendrils along the lateral edges of the oral surface of the arms, especially in cirrate octopods (Figure 236*b*).

Body: Fleshy protuberances of skin that can be erected as papillae, usually dorsal to the eyes (Figure 253*a*).

Club = See Tentacular club.

Complex band or Stripe = A single irregular or multiple series of chromatophores forming a thick but distinct line.

Cone, conus = The spoon-like or cup-like conical posterior terminus of the gladius or cuttlebone; homologous to



FIGURES 1–4.—1, Arm crown (teuthoid). 2, Hectocotylus (ocopod). 3, Tentacular club (teuthoid). 4, Gladii (teuthoid). (From Roper et al., 1984.)

the phragmacone of fossil teuthoids (Figure 4).

Corneal membrane = The very thin, turgid, transparent membrane that covers the eyes of myopsid and sepioid cephalopods (Figure 5).

Cuttlebone = The calcareous, oblong, supporting plate in the dorsal part of the mantle of cuttlefishes (Figure 6).

Dactylus = The distal, terminal section of the tentacular club, often characterized by suckers of reduced size (Figure 5).

Diagonals = Short lines oriented at angles oblique to bands (bars) and stripes (streaks).

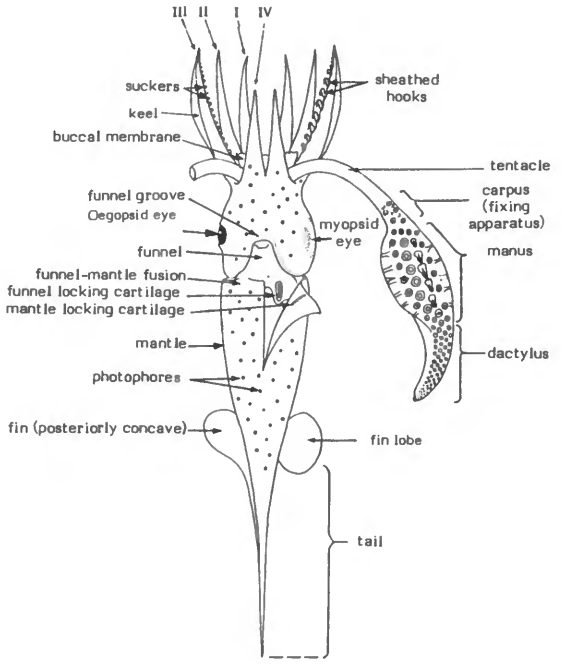
Fins = The muscular flaps that arise along the lateral or dorsolateral surfaces of the mantle of sepioids, teuthoids, vampyromorphs, and cirrate octopods; used for locomotion, steering, and stabilization (Figure 5).

Fin lobe = The portion of each fin that protrudes anteriorly from the anterior point of attachment of the fin to the mantle (Figure 5).

Fin angle = The angle between the longitudinal axis of the mantle and the posterior border of one fin (Figure 7).

Foveola = Transverse, membranous fold of skin that forms a pocket in the funnel groove of some oegopsids (Figure 8). See Side pockets.

Funnel = The ventral, subconical tube through which water is expelled from the mantle cavity during locomotion and respiration (reproductive and waste products, and the



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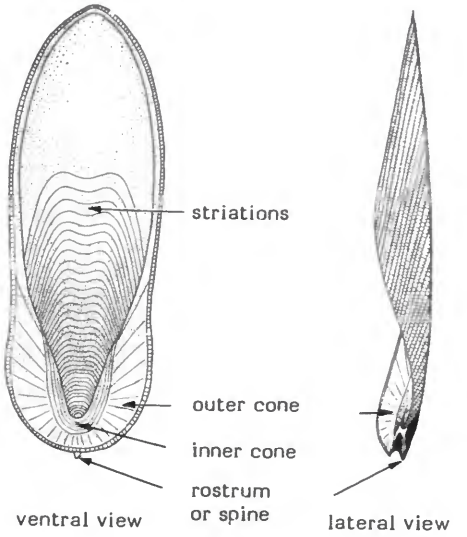

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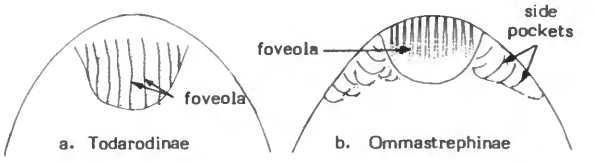

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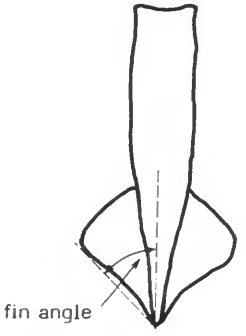

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FIGURES 5–9.—5, Composite diagram illustrating ventral view of basic squid (teuthoid) features. 6, Cuttlebone. 7, Fins and fin angle (teuthoid). 8, Funnel groove. 9, Funnel locking-cartilage patterns. (From Roper et al., 1984.)

ink also pass through the funnel) (Figures 5 and 14). (Archaic term: siphon.)

Funnel groove = The depression in the posteroventral surface of the head in which lies the anterior portion of the funnel (Figures 5 and 8).

Funnel locking-cartilage = The cartilaginous pad that contains variously shaped grooves, pits, pockets, or depressions on each ventrolateral side of the posterior part of the funnel that joins with the mantle component to lock the funnel and mantle together during locomotion. (Figures 5 and 9). See Mantle locking-cartilage.

Funnel organ = The glandular structure on the inside of the

funnel, generally a single W-shape form in octopods and a dorsal inverted V-shape component with opposed ventral oblong components in decapods (Figure 10).

Funnel valve = The semilunar muscular flap, a one-way valve, on the inner, dorsal surface near the distal opening of the funnel (Figure 10).

Gill lamellae = The leaf-like convoluted individual components of the gill through which gas exchange occurs (Figure 11).

Gill length = The longitudinal measure of the gill from the basal (proximal) filament to the distal tip.

Gills, Half-orange = In some cirromorphs the gills appear flattened because the tips of the demibranchs are free and radiate out from a broad central axis. In gills of this type the lamellae are arranged like the segments of a peeled orange half.

Gills = In decapods and octopods (other than cirromorphs) the gills are not flattened; the inner and outer demibranchs are attached to a narrow central axis and typically are arranged vertically in two diverging rows or are oriented parallel to the gill axis (lamellae perpendicular to axis). In sepioids the gills have free lamellae (not attached at tip) and have no branchial canal.

Gladius = The feather or rod-shape chitinous supporting structure in the dorsal midline of teuthoids and nonsepiid sepioids; the homolog of the shell of ancestral forms (Figure 4). Formerly termed pen.

Hectocotylus = One (or more) arm(s) of male cephalopods modified for transferring spermatophores to the female; modifications may involve suckers, sucker stalks, protective membranes, trabeculae, and arm shape (Figures 2 and 12). Not all species have a hectocotylus. See Calamus, Ligula.

Hooks = Chitinous, claw-like structures ontogenetically derived from the suckers on the arms and/or clubs of some oegopsids (Figure 3).

Infundibulum = The exposed flat, outer ring that forms the adhesive surface of the sucker.

Ink sac = The organ that manufactures and stores the ink of cephalopods; it generally lies along the intestine (sometimes imbedded in the digestive gland) and empties via a duct into the rectum.

Keel = (1) A flattened, muscular extension along the aboral surface of some arms to render them more hydrodynamic (Figure 5); (2) expanded muscular membrane on the aboral surface of the tentacular club of some groups (Figure 3).

Koelliker organs = Minute, bristle-like structures that cover the body of planktonic octopod larvae (see Figure 254*d,e*).

Lanceola = The expanded portion of the gladius vane.

Light organ = A simple or complex structure that produces bioluminescence by intrinsic (self-generated) or extrinsic (bacterial) means (Figures 5 and 13). Also termed photophore.

Ligula = The spatulate to spoon-shape, terminal structure of the hectocotylus of octopods, which includes the calamus proximally (basally) and usually a series of transverse ridges and grooves on the oral surface (Figure 2). See Calamus, Hectocotylus.

Macula = Irregular spot or splotch that is capable of expanding and contracting in size, typically the dark markings that surround the irridescent blue rings or lines on the body and arms of *Hapalochlaena*.

Mantle = The fleshy (muscular) tubular or sac-like body of cephalopods; contraction provides propulsion through jet-like expulsion of water as well as respiration; contains the viscera (Figures 5 and 14).

Mantle length (ML) = In decapods, measured dorsally from anterior most point of mantle to posterior apex of mantle or tip of united fins, whichever is longest. In octopods, measured dorsally from midpoint between eyes to posterior end of mantle. For exceptions, see Introduction.

Mantle locking-cartilage = The cartilaginous ridge, knob, or swelling on each side of the ventrolateral, internal surface of the mantle that locks into a corresponding funnel cartilage during locomotion (Figure 5). See Funnel locking-cartilage.

Manus = Central portion of club between the dactylus distally and the carpus proximally (Figure 5).

Needham's sac = The elongate, membraneous container at the terminus of the male reproductive tract that stores mature spermatophores (Figure 15) (= Spermatophore sac).

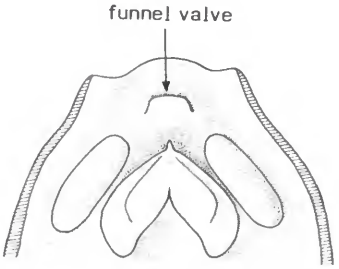
Nuchal cartilage = The oblong, cartilaginous plate on the posterodorsal surface of the head of most squids and cuttlefishes that articulates with a complimentary structure on the inner surface of the anterodorsal part of the mantle.

Nuchal folds = A series of longitudinal folds or pleats of skin on the nuchal region.

Nuchal region = The dorsolateral area around the posterior part of the head, normally covered by the anterior mantle wall.

Ocellus = Complex circular marking of fixed diameter in the integument of octopods, typically dark in contrast to body color, usually consisting of a dark pigmented center, with a concentric ring or other contrasting iridescent pattern, a dark pigmented outer ring, and finally a light narrow border. Located either on the web at the base of the second and third arms or on the posterior dorsal mantle of some octopods (Figure 14). Also referred to as a "false eye spot."

Olfactory organ = A pit, a bump, or a finger-like protuberance on the posterolateral surface of each side of the head;



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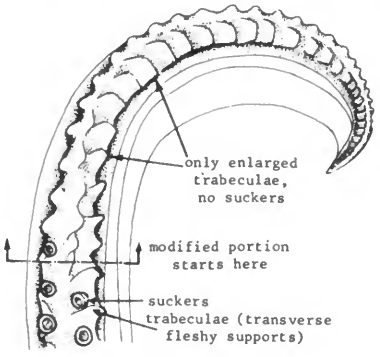

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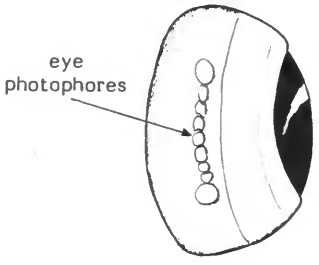

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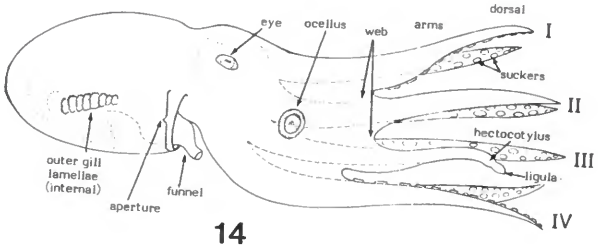

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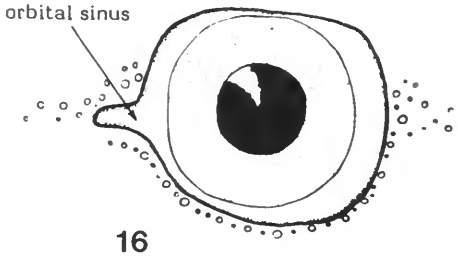

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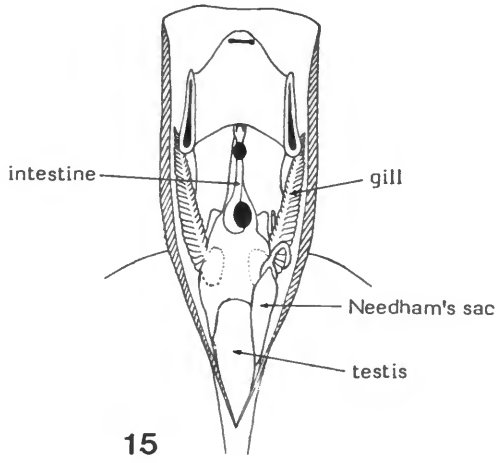

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FIGURES 10–16.—10, Funnel organ. 11, Gill lamella. 12, Hectocotylus (teuthoid). 13, Light organs (photophores). 14, Lateral view of octopod showing mantle. 15, Schematic internal view of anterior ventral mantle. 16, Orbital sinus of oegopsid eye. (From Roper et al., 1984.)

of presumed olfactory function.

Orbital pore = Minute pore in the skin, anterior to the cornea of sepioids and myopsids; remnent of the primary eyelids. See Orbital sinus.

Orbital sinus = An anteriorly directed indentation in the eyelid of oegopsids (Figure 16). See Orbital pore.

Pedicel = A cylindrical stalk that supports a sucker in sepioids and teuthoids (Figure 17).

Pen = See Gladius.

Photophore = An organ of greater or lesser complexity that produces and distributes bioluminescence, either intrinsically through biochemical reaction or extrinsically through luminescent bacteria (Figures 5 and 13). See Light organ.

Pocket, Tentacular = An open depression in the anteroventral surface of the head of sepioids into which the ejectable tentacles are retracted when not in use (Figure 18).

Protective membrane = Thin fold of integument along the lateral angles of the oral surface of the arms and clubs lateral to the suckers, usually supported by muscular rods called trabeculae (Figures 3 and 19). See Trabeculae.

Rachis = The thickened central axis that usually extends the entire length of the gladius. Free rachis is the portion that does not support vanes (Figure 4). See Gladius, Vane.

Radula = The chitinous, ribbon-like band in the mouth of cephalopods containing numerous transverse rows of teeth (Figure 20).

Radula, Ctenodont = A radula in which the rachidian (central) and lateral teeth are similar in appearance; each has multiple cusps (more than three). The central cusp (mesocone) on the rachidian tooth may be inconspicuous (Figure 235*e*).

Radula, Heterodont = A radula in which the teeth on each side are different from one another in appearance; the rachidian tooth has one or two cusps on either side of a distinct central cusp (mesocone), and each lateral tooth bears one or two cusps (Figures 20 and 235*c,d*).

Radula, Homodont = A radula in which all teeth appear similar in size and shape; each rachidian and lateral tooth has one simple cusp (see Figure 235*a,b*).

Ring = Well-defined circular line of color, generally formed by iridophores in the skin; typically the inside and outside of the ring are the same color and intensity as the body color.

Rostrum = See Spine.

Sepion = See Cuttlebone.

Side pockets = Small membranous folds of the integument that form pockets lateral to the foveola (Figure 8). See Foveola.

Simple band or Stripe = A single unbroken series of chromatophores forming a straight line.

Sperm receptacle = A bulbous structure in the buccal region of females of some species, e.g., loliginids, for the retention of viable sperm until they are required for fertilization. See Spermatophore pad.

Spermatophore = A tubular structure manufactured by male cephalopods for packaging sperm; each holds millions of sperm, being transferred intact, and attaching to the female until fertilization begins (Figure 21).

Spermatophore pad = A fleshy patch of tissue, usually in the mantle cavity of some female cephalopods (e.g., loliginids), to which sperm vesicles (discharged spermatophores) adhere after mating until fertilization occurs. See Sperm receptacle.

Spine = The sharp, spike-like extension on the posterior tip of the gladius or cuttlebone (Figures 4 and 6) (= Rostrum).

Spot = A regular color marking, typically circular, of fixed diameter that may occur anywhere on the body, may be either darker or lighter than the background color of the cephalopod. Dark spots consist of either single large chromatophores or clusters of small chromatophores, and light spots are defined by concentrations of leucophores in the skin.

Streak = A short longitudinal line of chromatophores that represents a broken or interrupted stripe.

Stripe = An unbroken longitudinal line or series of chromatophores; may be simple or complex.

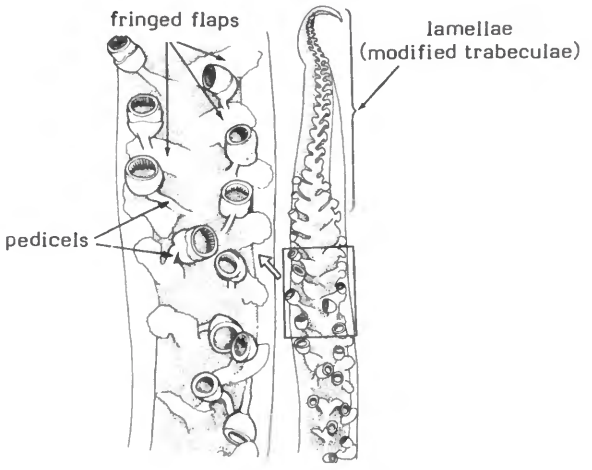
Suckers = Muscular, suction-cup structure on the arms and tentacles (rarely on the buccal membrane) of cephalopods; some are stalked, placed on muscular rods that contract (squids and cuttlefishes); some are sessile, embedded without stalks on the oral surface of the arms (octopuses) (Figure 22*a*). They are usually counted either in longitudinal or in transverse (oblique) rows (Figure 22*b*).

Sucker ring = Chitinous, often serrated or denticulate ring that encircles the opening of suckers of squids and cuttlefishes (Figure 23).

Swimming membrane = An elongate, muscular vane along the aboral surface of some arms of cephalopods that functions to streamline and support the arms during swimming (Figures 3 and 5). See Keel.

Tail = The posterior extension generally of the gladius and mantle epithelium, frequently elongate. Fins may extend posteriorly along the tail (Figure 5), and the tail may be swollen by the inclusion of vacuolated tissue.

Tentacles = Elongate, fourth circumoral appendages of cuttlefishes and squids used to capture prey; divided into a proximal stalk and a distal club; clubs generally expanded with arrangement of suckers (or hooks); stalks commonly devoid of suckers. Tentacles can



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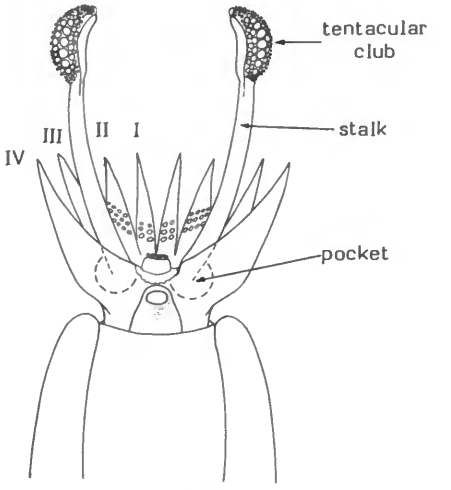

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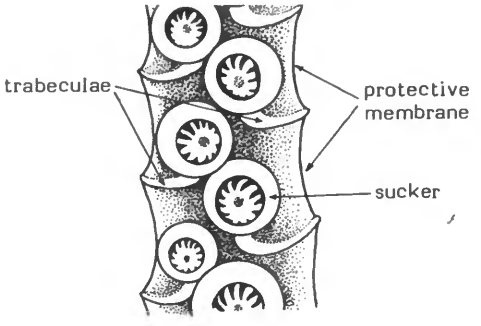

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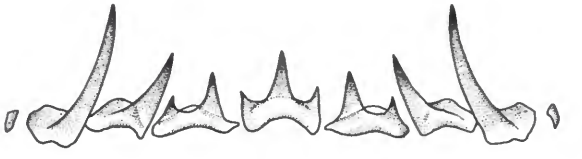

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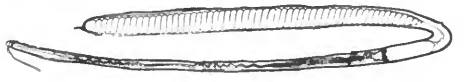

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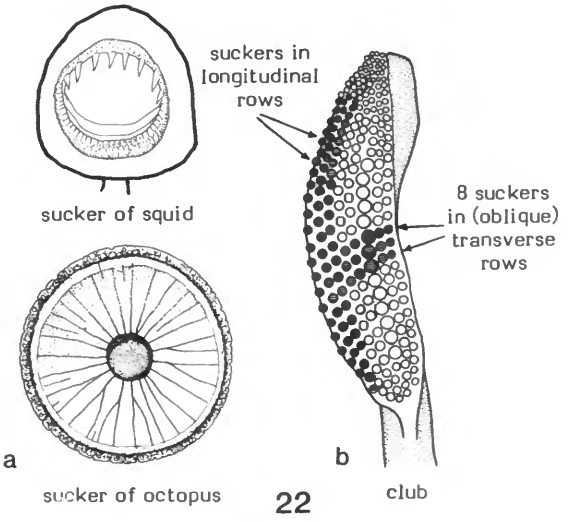

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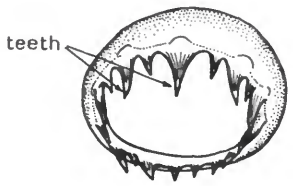
FIGURES 17–22.—17, Hectocotylized arm in males. 18, Ventral diagrammatic view of cuttlefish features. 19, Sculpture features of squid arm. 20, Radula. 21, Spermatophore. 22, Examples of suckers. (From Roper et al., 1984.)



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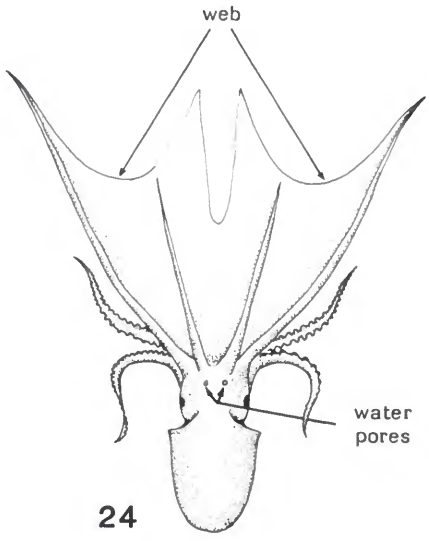

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FIGURES 23, 24.—23, Sucker ring. 24, Water pores. (Both from Roper et al., 1984.)

retract into pockets on the head of cuttlefishes, or merely contract, as in squids (Figures 5 and 18).

Tentacular club = Terminal portion of a tentacle; armed with suckers (or suckers and/or hooks), used for capturing prey (Figures 3, 5, and 18).

Trabeculae = Muscular rods that support the protective membranes on the arms and clubs of cephalopods; occasionally membranes are reduced and/or trabeculae are elongated, so they extend beyond the edge of the membrane, papilla-like (Figure 19).

Tragus = A small, cartilaginous, knob-like projection from the inner wall of the funnel locking-cartilage in some families (e.g., Chiroteuthidae, Mastigoteuthidae). See Antitragus.

Vane = A thin lateral expansion of the gladius that arises from the rachis (Figure 4). See Rachis.

Water pores = Small orifices at the base of the web of some pelagic octopuses, e.g., *Tremoctopus* (Figure 24).

Web = A thin, muscular fold of skin of greater or lesser extent that extends between the arms of many octopuses and a few squid, giving an umbrella-like appearance when the arms are spread, e.g., cirroteuthids, histioteuthids (Figures 14 and 24).

Provisional Key to Young Stages of Cephalopods

This provisional key is designed to help identify young stages of the families of cephalopods. Several points must be kept in mind when using a dichotomous key of this kind because there are limitations to its effectiveness. First, it is entirely artificial, and it does not imply phylogenetic relationships; thus, for example, families in different orders might appear together in a couplet because they show a similar character. The characters used in the key are not necessarily the most important systematic familial characters, or even the most conspicuous; they simply are those characters that allow separation from other families presented in that section of the key. Second, the key is designed primarily for identification of earliest "larval" stages from hatchlings to approximately 10 mm ML. However, the user is cautioned that equivalent small sizes are not available for all groups, so some key characters might not apply to hatchlings and smallest stages. However, with a large enough size range of specimens, it should be possible to identify larger forms, then work back through the juveniles to "larval" stages. The smallest known specimens in a given family or genus are indicated in the text for each family. In fact, in some families the smallest known specimens are juveniles of 20–60 mm ML, e.g., Architeuthidae, Batoteuthidae. Third, some families are known from only a very few specimens, and their systematics are poorly understood, e.g., Batoteuthidae, Promachoteuthidae. Exclusive reliance on the key for identification of cephalopod "larvae" is not recommended. To confirm identifications, refer to taxonomic diagnoses, illustrations, and if possible, additional literature cited under each family.

While the key is primarily for identification to families, practical considerations, e.g., overlapping characters, unknown "larval" characters, or a lack of material, have resulted in the keying out of some subfamilies and genera. Occasionally in groups where young stages are not well known, the key will lead to two families that seem poorly differentiated, e.g., Architeuthidae, Neoteuthidae. In such cases, even more reliance on original descriptions and illustrations is necessary. Keys to adults of teuthoid families might be helpful (see review in Roper et al., 1969; Nesis, 1987).

Finally, as a note of encouragement, especially to workers not specialists in cephalopod taxonomy, it is entirely reasonable to expect that not every specimen in a given collection can be identified to the desired taxonomic level. We still have much to learn before all cephalopods at all stages can be identified, and this key and manual are an attempt to help workers toward this goal.

1. Mantle without fins or fin rudiments [Figure 25*a*] 36
   Mantle with fins or fin rudiments [Figure 25*b*] 2
2. Mantle with lateral fins [Figure 26*a*] 3
   Mantle with subterminal or terminal fins or fin rudiments [Figure 26*b*]; or dorsally attached fins [Figure 28*a*] 4
3. Arm crown with 8 subequal arms with suckers only (cirri develop in later juvenile stage) [Figure 27*a*] . . . . . CIRRATA
   Arm crown with 6–8 arms and 2 tentacles between arms III and IV; all appendages with stalked suckers [Figure 27*b*] 5
4. Fins insert near dorsal midline of posterior mantle; 8 arms of smallest specimens with cirri only, no suckers; suckers stalked when they develop; retractile velar filaments without cirri or suckers present between arms I and II; a second pair of fins develops anterior to first pair (~15 mm ML) [Figures 28*a*, 234] . . . . . VAMPYROMORPHA
   Fins insert dorsolaterally or laterally on mantle [Figure 28*b*]; arms with no cirri and with stalked suckers; no velar filaments; only one pair of fins (except Chiroteuthidae) 6
5. Fins long and narrow (not paddle-shape); extend laterally from near posterior end to near anterior margin of mantle, but never united posteriorly [Figure 29*a*] . . . . . SEPIIDAE
   Fins paddle- or ear-shape [Figure 29*b*] 7

6. Coiled chambered shell in posterior mantle; tiny fins or fin rudiments widely separated and perpendicular to body axis; buccal mass huge, with well-developed beaks that reach beyond short arms; arm crown development incomplete [Figure 30*a*] . . . . . SPIRULIDAE
   No coiled chambered shell; buccal mass inconspicuous [Figure 30*b*] 8
7. Each fin longer (antero-posteriorly) than wide [Figure 31*a*] . . . SEPIADARIIDAE
   Each fin at least as wide as long (antero-posteriorly) [Figure 31*b*] . . SEPIOLIDAE
8. Arm crown with 8 arms, second pair longest; tentacles not developed at hatching [Figure 32] . . . . . IDIOSEPIIDAE
   Arm crown with 4–8 arms; tentacles (may be fused) at least as long as longest arms 9
9. Tentacles fused into "proboscis" in young stages [Figure 33*a*]; funnel locking-cartilage inverted T-shape . . . . . OMMASTREPHIDAE
   Tentacles never fused [Figure 33*b*]; funnel locking-cartilage not inverted T-shape 10
10. Eye entirely covered by transparent membrane (cornea) [Figure 34*a*] 11
    Eye not entirely covered by transparent membrane (at least eye lens in contact with sea water in living animals) [Figure 34*b*] 12
11. Tentacular clubs with 4 rows of suckers [Figure 35*a*] . . . . . LOLIGINIDAE
    Tentacular clubs with 2 rows of suckers [Figure 35*b*] (tentacles absent at hatching) . . . . . PICKFORDIATEUTHIDAE
12. Fins with muscular ribs; tentacles stumpy; clubs spatulate, round, out-turned; single chromatophore on aboral surface of club [Figure 36*a*] . . . CTENOPTERYGIDAE
    Fins without ribs [Figure 36*b*] 13
13. Head with long neck [Figure 37*a*] 14
    Head without long neck [Figure 37*b*] 15
14. Neck with dorsal hump, with single chamber; mantle without conspicuously long tail; arm crown stalk absent [Figure 38*a*] . . . . . BRACHIOTEUTHIDAE
    Neck without hump, with multiple irregular chambers; tail long with secondary fin; base of arm crown elongated to form arm crown stalk [Figure 38*b*] . . . . . CHIROTEUTHIDAE
15. Light organs at base of arms (inconspicuous) [Figure 39*a*] . . BATHYTEUTHIDAE
    Light organs absent at base of arms [Figure 39*b*] 16
16. Transverse T-shape funnel locking-cartilage [Figure 40*a*]; chromatophores dense on mantle . . . . . THYSANOTEUTHIDAE
    Straight, round, or subtriangular funnel locking-cartilage [Figure 40*b*]; chromatophores less dense 17
17. Mantle fused to funnel locking-cartilage [Figure 41*a*] 18
    Mantle not fused to funnel locking-cartilage [Figure 41*b*] 19
18. Mantle free in nuchal region [Figure 42*a*] . . . . . GRIMALDITEUTHIDAE
    Mantle fused in nuchal region [Figure 42*b*] . . . . . CRANCHIIDAE
19. Mantle fused in nuchal region; fins large broad terminal, joined posteriorly [Figure 43]; photophores absent . . . . . PROMACHOTEUTHIDAE
    Mantle free in nuchal region [Figure 42*a*]; fins not terminal or joined (terminal in Histioteuthidae but not large broad); photophores may be present 20
20. Fourth arms absent or rudimentary 21
    Fourth arms developed 22
21. Tentacular club suckers in four rows [Figure 44*a*] . . . . . ONYCHOTEUTHIDAE
    Tentacluar club suckers in more than four rows [Figure 44*b*] . . . . GONATIDAE
22. Body elongate with long pointed tail; tentacles greatly enlarged or elongate [Figure 45*a*] 23
    Body without long pointed tail; tentacles not conspicuously enlarged or elongate [Figure 45*b*] 25

23. Arms elongate, with more than 2 rows of suckers; funnel locking-cartilage oval without tragus and antitragus . . . . . JOUBINITEUTHIDAE
Arms not elongate, with 2 rows of suckers; funnel locking-cartilage simple straight or oval with tragus 24
24. Funnel locking-cartilage simple straight [Figure 46*a*] . . . . . BATOTEUTHIDAE
Funnel locking-cartilage oval with tragus [Figure 46*b*] . . . MASTIGOTEUTHIDAE
25. Eyes stalked, tubular, anterolaterally directed [Figure 47*a*] 26
Eyes not stalked, tubular, or anterolaterally directed [Figure 47*b*] 27
26. Tentacles rudimentary or absent; club suckers fewer than 12 . . . . . OCTOPOTEUTHIDAE
Tentacles developed; club suckers more than 12 . . . . . CYCLOTEUTHIDAE
27. Integumental light organs around margin of eye lid [Figure 48*a*] . . . . . HISTIOTEUTHIDAE
Integumental light organs absent around eye lid [Figure 48*b*] 28
28. Light organs present on eye, viscera, and/or mantle 29
Light organs absent 33
29. Light organs on eye well defined [Figure 49*a*] 30
Light organs absent on eye [Figure 49*b*] . . . . . ANCISTROCHEIRIDAE (enoploteuthid group)
30. Light organs absent on viscera . . . . . ENOPLOTEUTHIDAE
Light organs present on viscera 31
31. Ventral surface of eye with 3–5 light organs, central one develops first, always enlarged [Figure 50*a*] . . . . . LYCOTEUTHIDAE
Ventral surface of eye with subequal light organs [Figure 50*b*] . . . . . PYROTEUTHIDAE (enoploteuthid group)
32. Tentacular club suckers in more than 4 rows [Figure 44*b*]; no minute papillae on mantle 33
Tentacular club suckers in four rows [Figure 44*a*]; minute papillae on mantle 35
33. Carpal suckers/buds numerous minute in a cluster [Figure 51*a*]; fin attachment dorsolateral, divergent especially anteriorly [Figure 51*b*] 34
No numerous minute suckers on carpus [Figure 51*c*]; fin attachment dorsal, not divergent . . . . . PSYCHROTEUTHIDAE
34. Carpal suckers/buds few, not minute suckers . . . . . ARCHITEUTHIDAE
Carpal suckers numerous . . . . . NEOTEUTHIDAE
35. Tentacular club suckers numerous, laterally compressed [Figure 52*a*] . . . . . PHOLIDOTEUTHIDAE
Tentacular club suckers few (up to 6), poorly differentiated [Figure 52*b*] . . . . . LEPIDOTEUTHIDAE
36. Body gelatinous, transparent, often with jelly-like coat [Figure 53*a*] 37
Body muscular, opaque [Figure 53*b*] 40
37. Eyes spindle-shape in side view; suckers uniserial within web, biserial beyond web [Figure 54*a,b*] . . . . . ALLOPOSIDAE
Eyes other than spindle-shape; suckers uniserial throughout [Figure 54*c*] . . . 38
38. Eyes tubular, antero-dorsally directed [Figure 55*a,b*] . . . . . AMPHITRETIDAE
Eyes rectangular or elliptical, laterally directed [Figure 55*c,d*] 39
39. Eyes rectangular; digestive gland elongate, tapered posteriorly to a point, extends length of mantle [Figure 56*a,b*] . . . . . VITRELEDONELLIDAE
Eyes elliptical; digestive gland round to oval, less than half length of mantle [Figure 56*c,d*] . . . . . BOLITAENIDAE
40. Specialized funnel locking-cartilage present (a) *Argonauta*, (b) *Ocythoe*, (c) *Tremoctopus*; either right or left arm III modified in young males (mature males dwarfed in relation to size of females) [Figure 57*a–d*] 41

Specialized funnel locking-cartilage absent [Figure 57*e Octopus*]; arms not modified in young males (mature males and females about equal in size) [Figure 57*f*] OCTOPODIDAE 46

41. Arms I and IV greatly enlarged; arms not enclosed in circumbrachial membrane; ventral mantle of females reticulate with interconnecting tubercles and ridges [Figure 58*a*] . . . . . OCYTHOIDAE

Arms other than above; circumbrachial membrane partially or entirely encasing arms in hatchlings smaller than 2 mm ML; ventral mantle not reticulate [Figure 58*b*] 42

42. Mantle length 2 mm or less 43

Mantle length greater than 2 mm 44

43. Arms I greatly elongated, robust; arms III greatly reduced [Figure 59*a*] (see couplet 45) . . . . . TREMOCTOPODIDAE

Arms equal or, in females, arms I slightly elongate [Figure 59*b*] (see couplets 44 and 45) . . . . . ARGONAUTIDAE

44. Arms I enlarged; arms III, if modified in male, on right side [Figure 60*a*] . . . 45

Arms subequal; left arm III modified in male, enclosed in sac [Figure 60*b*] . . . . . ARGONAUTIDAE

45. Arms II enlarged (equal to arms I by 6 mm ML); "flag-like" membrane at ends of arms I absent [Figure 61*a*] . . . . . TREMOCTOPODIDAE

Arms II not enlarged; "flag-like" membrane at ends of arms I in female [Figure 61*b*] . . . . . ARGONAUTIDAE

46. One or more arm pairs elongate 47

All arms short, subequal in length [Figure 62] 48

47. Only arms III elongate; mantle generally sac-like, rounded posteriorly [Figure 63*a*] . . . . . **"macrotritopus type"**

All arms elongate, especially arms I and II; mantle generally elongate, tapering posteriorly [Figure 63*b*] . . . . . **"teuthoides type"**

48. Suckers always in single row [Figure 64*a*] . . . . . ELEDONINAE

Suckers alternate or in double row (>2–3 mm ML and 5 or more suckers per arm) [Figure 64*b*] . . . . . OCTOPODINAE

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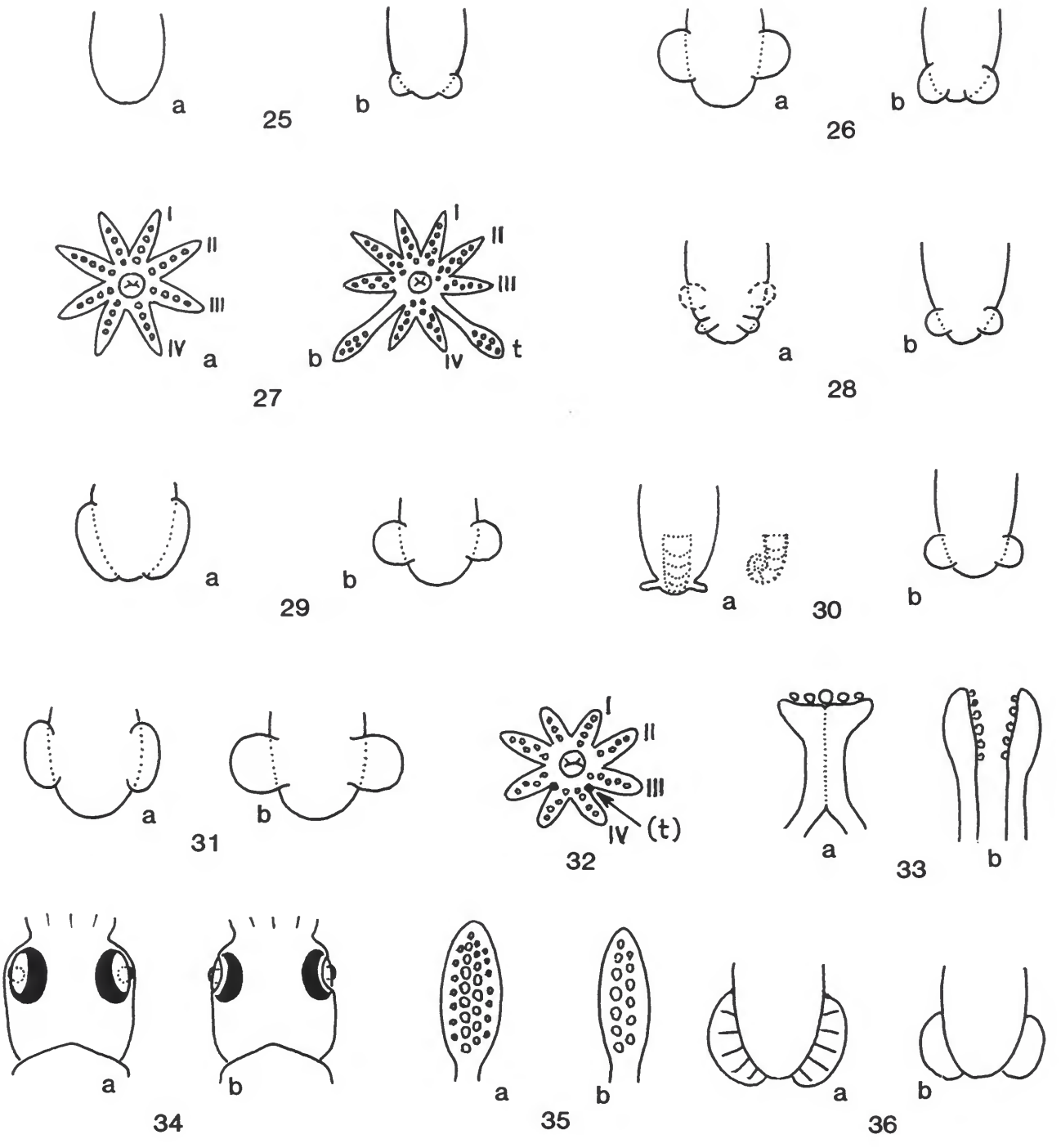
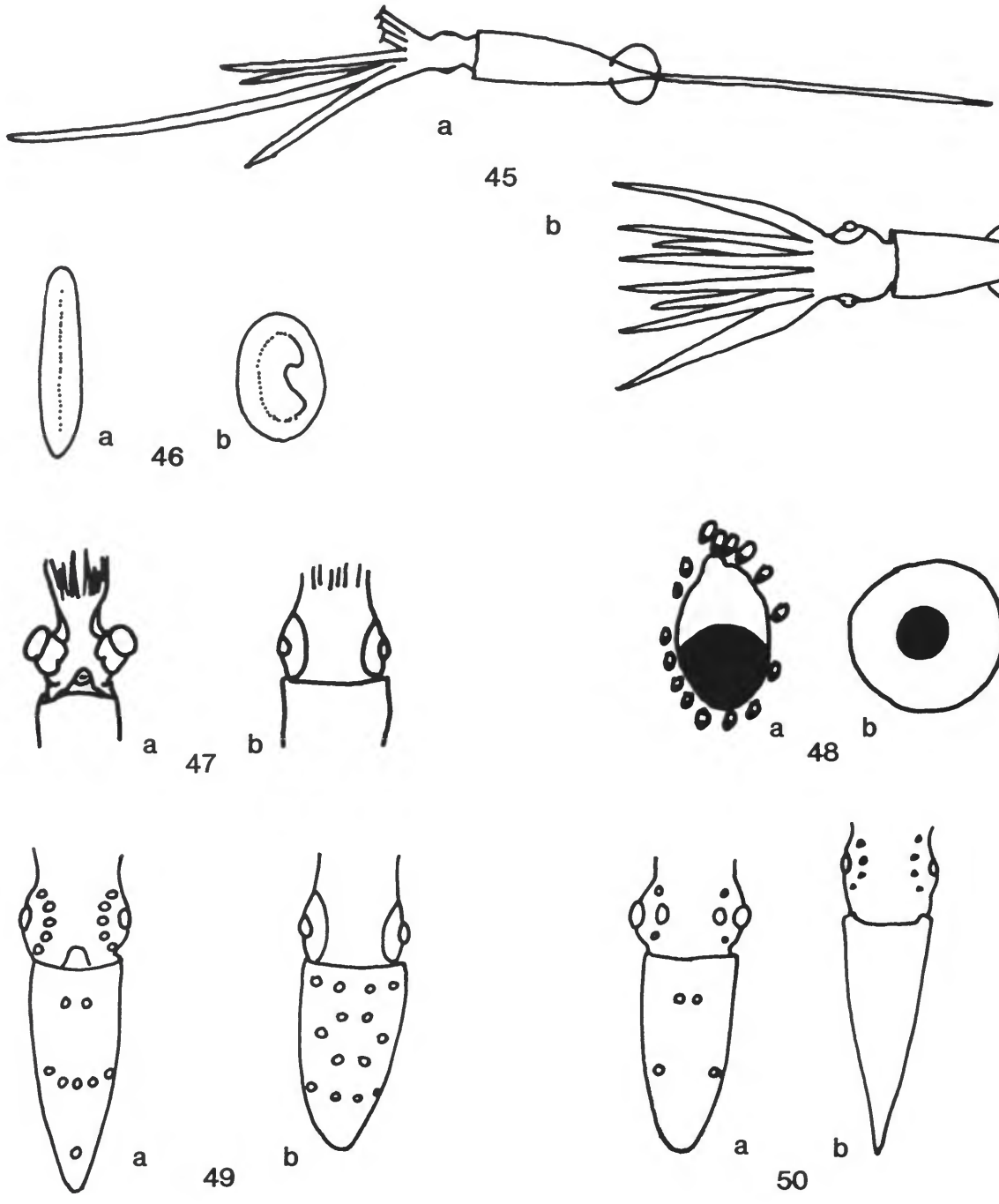
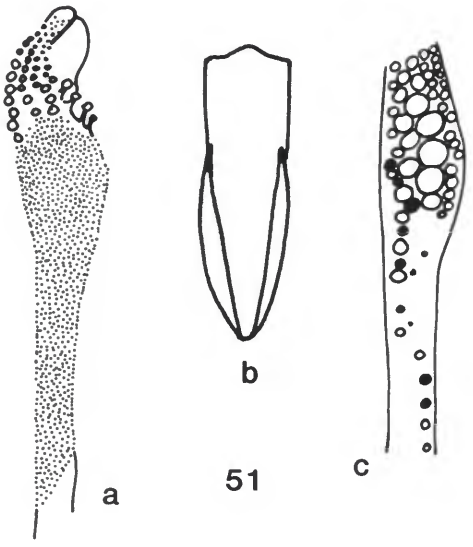


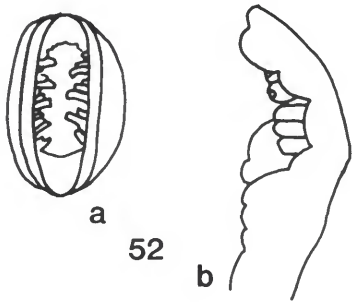
FIGURES 25-36.—Illustrations of characters in the "Key to Young Stages of Cephalopods."

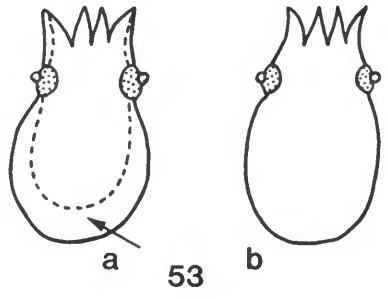
FIGURES 37-44.—Illustrations of characters in the "Key to Young Stages of Cephalopods" (cont.).

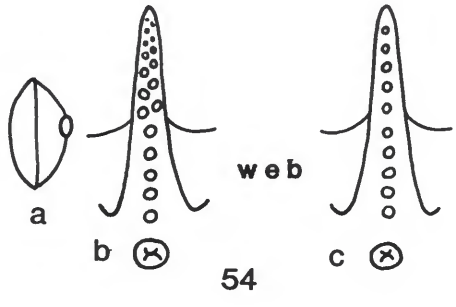


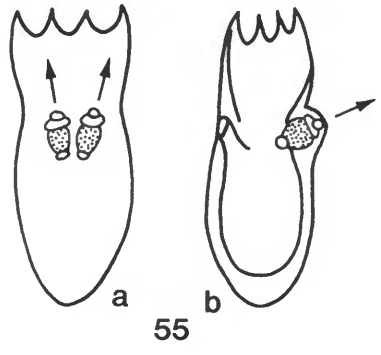
FIGURES 45-50.—Illustrations of characters in the "Key to Young Stages of Cephalopods" (cont.).

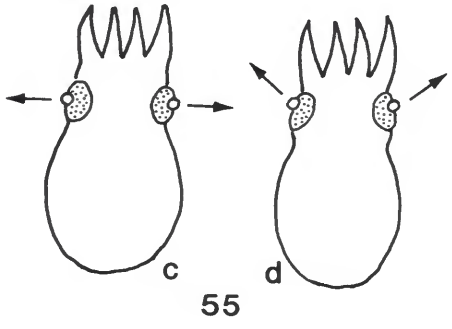


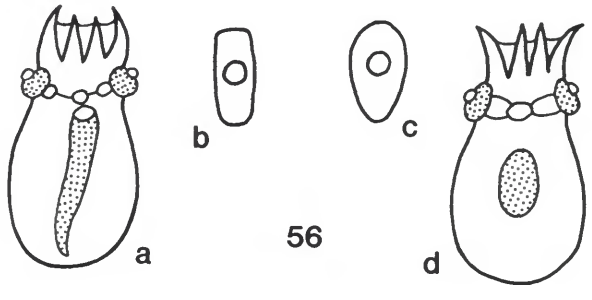




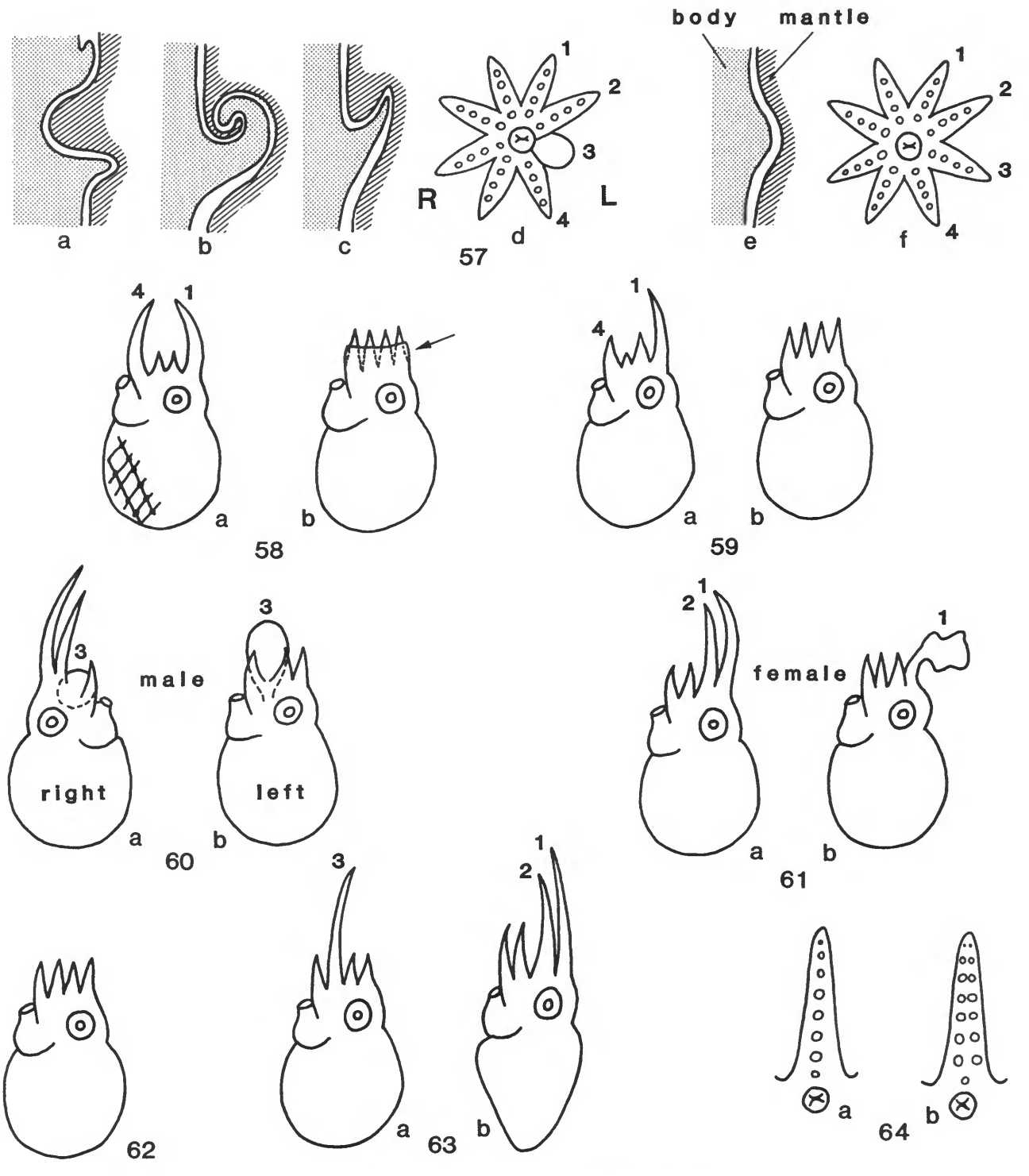








FIGURES 51–56.—Illustrations of characters in the "Key to Young Stages of Cephalopods" (cont.).



FIGURES 57–64.—Illustrations of characters in the "Key to Young Stages of Cephalopods" (cont.).

Family Accounts

Order SEPIOIDEA Naef, 1916

(by C.C. Lu, A. Guerra, F. Palumbo, and W.C. Summers)

ORDINAL CHARACTERS.—Shell calcareous (*Sepia, Spirula*), or chitinous (sepiolids), or absent. Ten circumoral appendages; tentacles retractile into pockets (Sepiidae); suckers with chitinous rings; posterior fin lobes free, not connected at midline; eyes covered with a cornea (except *Spirula*); gills without branchial canal between afferent and efferent branchial blood vessels; digestive gland paired; each tooth of radula with a single cusp; buccal membrane present; olfactory organ a ciliated pit or flat wart partially covered by protective epithelium.

To the best of our knowledge members of this order hatch out as miniature adults (except *Spirula*), i.e., with most adult characters present in the newly hatched young. The characters used for identification of juveniles are, therefore, similar to those used for identifying adults.

Key to Families of SEPIOIDEA

Table 1 presents a summary of the familial characters of the Sepioidea.

1. Shell calcified 2
   Shell chitinous or lacking 3
2. Internal shell coiled, chambered [Figure 65] . . . . . SPIRULIDAE
   Internal shell straight, laminate [Figure 68] . . SEPIIDAE
3. Eye open 4
   Eye covered by cornea [Figure 69] . . . . IDIOSEPIIDAE
4. Mantle-funnel locking-cartilage simple, straight [Figure 70] . . . . . SEPIOLIDAE
   Mantle-funnel locking-cartilage absent; dorsal mantle margin fused to head, ventral mantle margin fused to funnel [Figure 71] . . . . . SEPIADARIIDAE

REFERENCES.—Naef (1923), Roper et al. (1984).

Family SPIRULIDAE Owen, 1836

FAMILY CHARACTERS.—Monotypic family.

Spirula spirula (Linne, 1758)

SPECIES CHARACTERS (Figures 65–67).—Internal shell calcified, coiled, and chambered; characteristic shell at 1.5 mm ML; newly hatched with 2–3 shell chambers; mature egg size 1.5–1.7 mm (Chun, 1914; Bruun, 1943).

GEOGRAPHICAL DISTRIBUTION.—Worldwide in tropical and subtropical waters at temperatures above 10°C; associated with continental slope and oceanic islands.

VERTICAL DISTRIBUTION.—A vertical migrator at 100–300 m at night to 500–700 m (occasionally to 950 m) during daytime.

REMARKS.—See Naef, 1923:512, fig. 279 for posterior mantle muscle attachment.

REFERENCES.—Bandel and Boletzky (1979), Bruun (1943), Clarke (1966, 1969, 1970), Herring et al. (1981), Naef (1923), Thomas and Bingham (1972).

Family SEPIIDAE Keferstein, 1866

FAMILY CHARACTERS.—Cuttlebone (shell or sepion) internal, usually chalky (calcareous), porous, finely laminate; mantle broad, robust, oval to circular in outline, slightly flattened dorsoventrally; fins narrow, lateral, occupy almost entire mantle length; posterior fin lobes free, not connected at midline; arms with 2–4 rows and tentacles with 4–8 or more longitudinal rows of suckers; tentacles retractile into pockets on ventrolateral sides of head; funnel locking-apparatus curved to angular, not straight.

GEOGRAPHICAL DISTRIBUTION.—Temperate to tropical waters in Old World; absent from the Americas.

VERTICAL DISTRIBUTION.—Nectobenthic (demersal), on continental shelf and upper slope from 0–500 m.

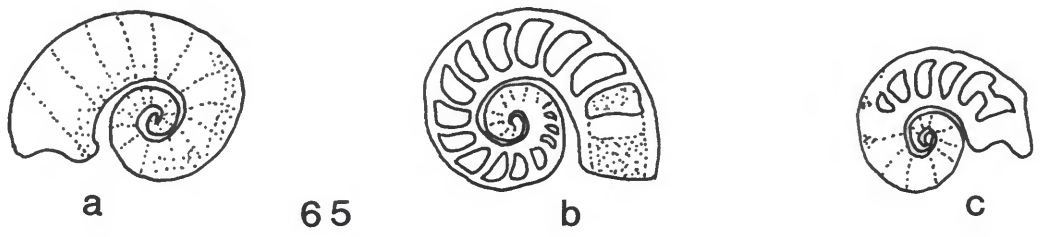
REMARKS.—Some species of *Sepia* have a spine at posterior end of shell; in *Hemisepius* species the dorsal shield of the cuttlebone is not calcified. (See Figure 74 for comparisons of some species of hatchlings of *Sepia*.) In Sepiidae mature adult sizes range from 20 to 500 mm ML; greatest egg size around 10 mm; smallest egg size unknown but likely to be only 1 to 2 mm.

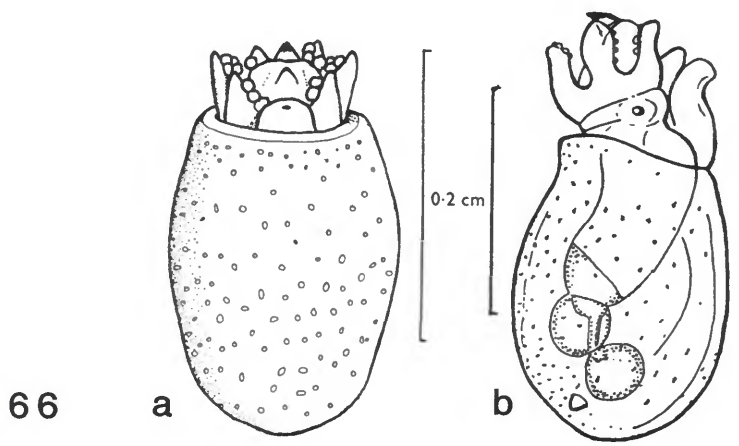
Key to Genera of SEPIIDAE

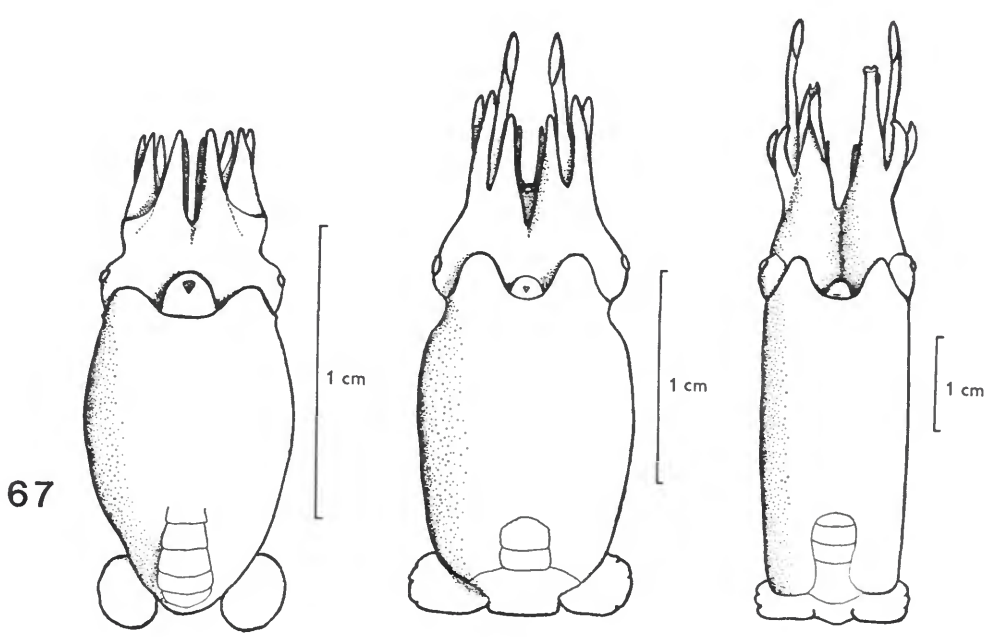
1. Glandular pore at posterior end of mantle between fins [Figure 72*a*] . . . . . ***Sepiella***
   No glandular pore at posterior end of mantle [Figure 73*a*] 2
2. Locking-cartilage with tubercle on mantle component and corresponding depression on funnel component [Figure 73*c*] . . . . . ***Sepia***
   Locking-cartilage semicircular without tubercle on mantle component and without corresponding depression on funnel component . . . . . ***Metasepia***

TABLE 1.—Summary of characters of Sepioidea.

Taxon	Shell	Mantle-funnel locking-cartilage	Dorsal mantle margin	Arm web 1/2 arm length	Mantle form	Fin shape & position	Ink sac light organ	Sucker rows on club	Benthic habitat	Geographic distribution	No. of species	Remarks
SPIRULIDAE	Coiled, chambered	Simple & straight	Free	–	Elongate, cylindrical	Terminal	No	12	Yes	Worldwide	1	Fins set diagonal to body axis
Spirula												
SEPIIDAE	Straight, laminate		Free	–	Oval to circular	Terminal-lateral	No		Yes	Not in Americas		
Sepia		Semicircular						8–24			120	
Sepiella		Triangular						8–24			7	Glandular pore at posterior end of body
Metasepia		Absent						5			2	
SEPIADARIIDAE	Absent		Fused	–	Short, rounded	Lateral	No		Yes	Indo-West Pacific		
Sepiadarium		Fused						6–8			5	
Sepioloidea		Shoe-sole shape						6–24			2	
SEPIOLIDAE	Chitinous	Simple & straight			Short, rounded							
ROSSIINAE			Free	Between III & IV		Lateral			Yes			
Rossia							No	6–numerous		Worldwide	14	
Semirossia							Bilobed	6–8		Western Atlantic	3	
Neorossia							No	6–7		Northeast Atlantic	1	Ink sac greatly reduced, non-functional
HETEROTEUTHINAE	Chitinous	Simple & straight		All except between arms IV	Short, rounded	Lateral	Round to oval		No			
Heteroteuthis			Free					Numerous		Worldwide	4	
Nectoteuthis			Free					Numerous		Caribbean	1	
Iridoteuthis			Fused					Numerous		Pacific	2	Prominent cutaneous fold or ridge on dorsal mantle
Stoloteuthis			Fused					8–?		Atlantic	1	Dorsal mantle-head fusion broad
Sepiolina			Fused					16		Indo-Pacific	1	
SEPIOLINAE	Chitinous	Simple & straight	Fused	Between III & IV	Short, rounded	Lateral			Yes			
Sepiola							Bean-shape	Up to 8		Worldwide	14	
Euprymna	Absent						Saddle-shape	Numerous		Indo-West Pacific	8	
Rondeletiola							Lens-shape	16		Mediterranean & eastern Atlantic	1	
Sepietta							No	16–32		Not in Pacific	3	
Inioteuthis							No	8–10		Indo-West Pacific	3	
IDIOSEPIIDAE	Chitinous	Deep oval or simple & straight	Free	–	Cylindrical, blunt	Terminal	No	2–4	–	Indo-West Pacific		Previously *Idiosepius* was considered to lack a gladius, but presence of a delicate gladius has been found (Boletzky, unpub. data).
Idiosepius											7	







FIGURES 65–67.—*Spirula spirula*: 65*a–c*, external and internal views of shell (from Bruun, 1943). 66, Views of very young specimens showing huge buccal mass and small fin rudiments (from Clarke, 1966): *a*, ventral; *b*, lateral. 67, Ventral view of later stages (from Clarke, 1970).

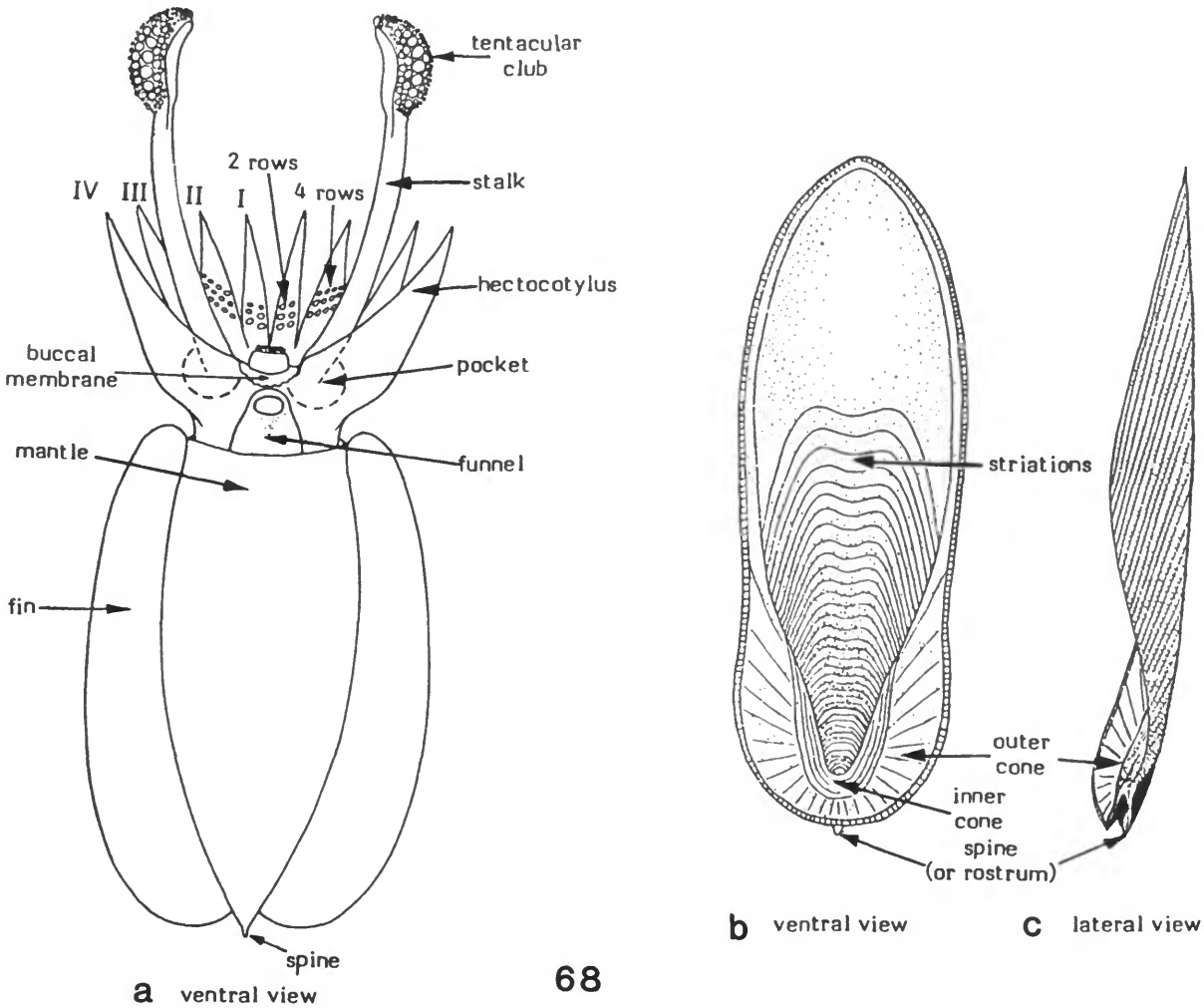
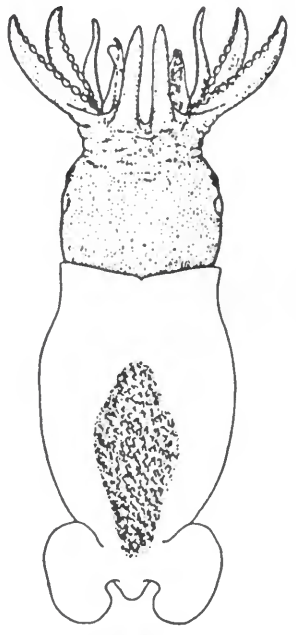


FIGURE 68.—Sepiidae: *a*, schematic representation of cuttlefish features; *b,c*, cuttlebone features. (From Roper et al., 1984).

FIGURES 69–73 (opposite page).—69, Idiosepiidae: dorsal view of adult *Idiosepius* (from Roper et al., 1984). 70, Sepiolidae: funnel locking-cartilage of *Euprymna tasmanica* (Lu, unpublished). 71, Sepiadariidae: dorsal view of adult *Sepiadarium kochi* (from Roper et al., 1984). 72, Sepiidae, *Sepiella: a*, ventral view of adult; *b*, cuttlebone (from Roper et al., 1984); *c*, locking apparatus (from Roeleveld, 1972). 73, Sepiidae, *Sepia: a*, ventral view of adult; *b*, cuttlebone (from Roper et al., 1984); *c*, locking apparatus (from Roeleveld, 1972).



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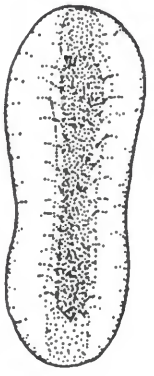

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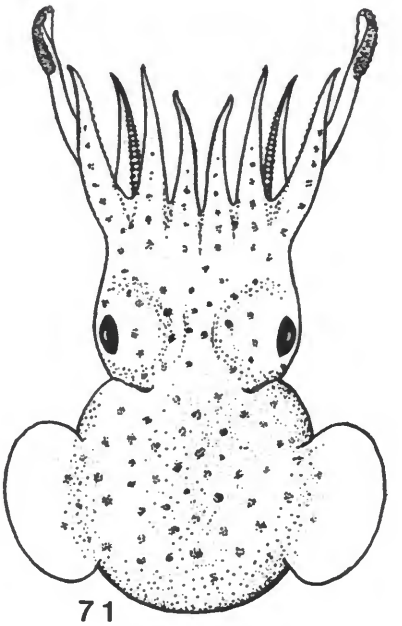

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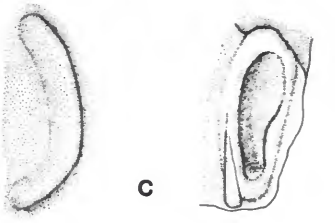

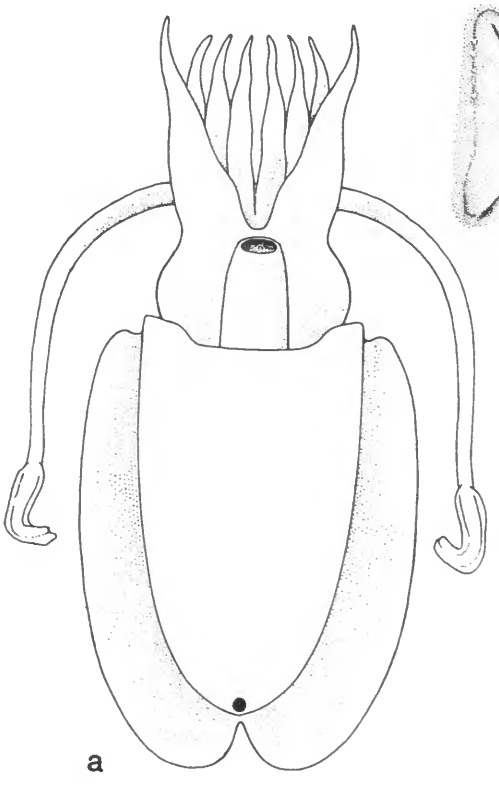

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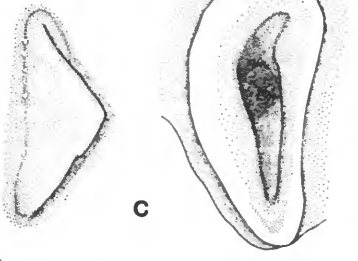

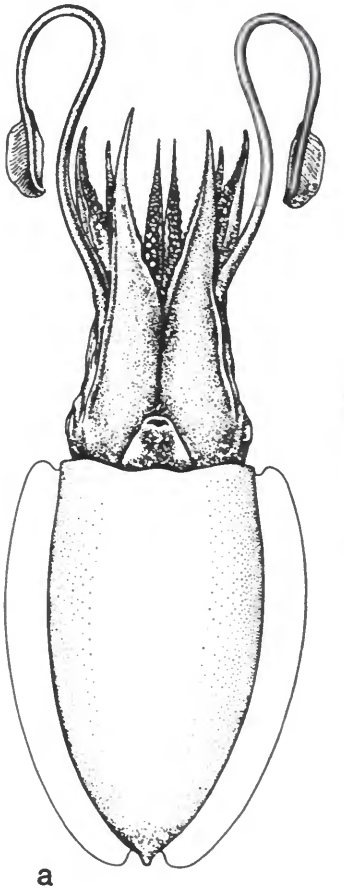

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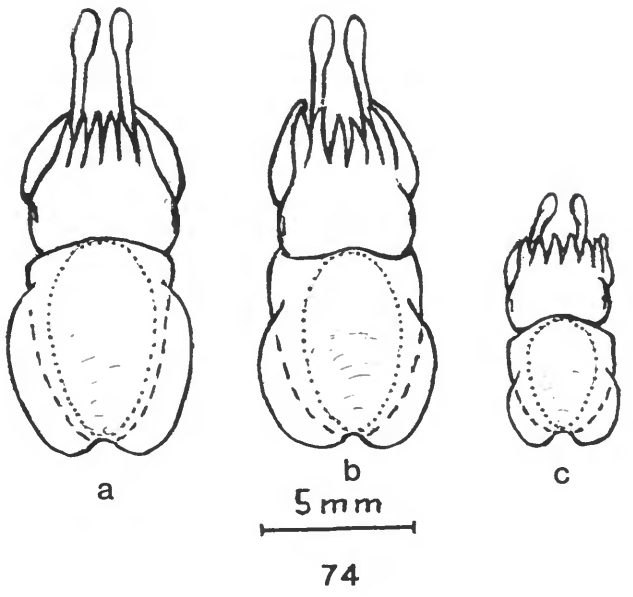
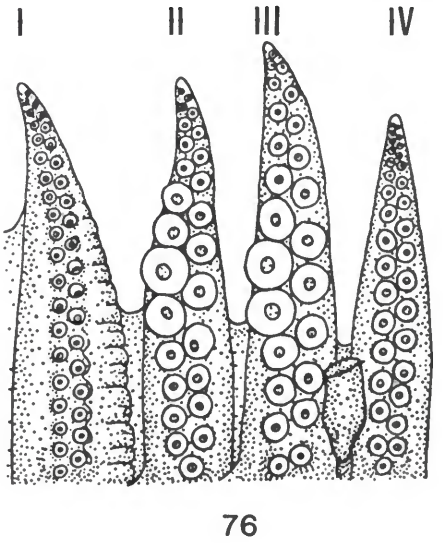
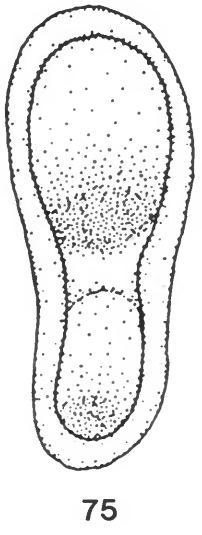
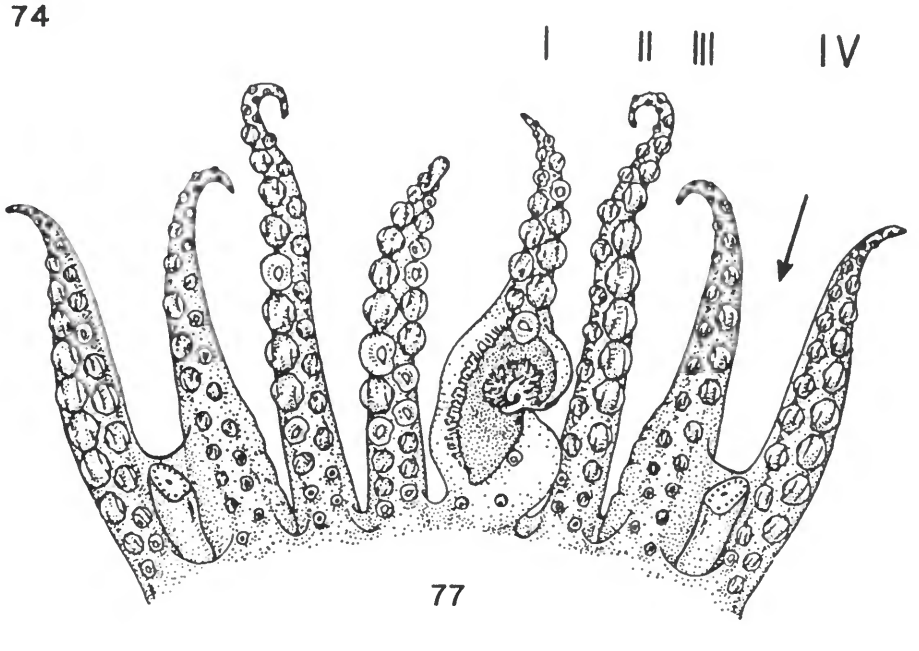








FIGURES 74–77.—74, Sepiidae, dorsal view of hatchlings: *a, Sepia officinalis; b, S. orbignyana; c, S. elegans;* dotted line indicating outline of cuttlebone (Boletzky, unpublished). 75, Sepiadariidae, *Sepioloidea lineolata:* funnel locking-cartilage (Lu, unpublished). 76, Heteroteuthinae, *Sepiolina nipponensis:* spread left half of arm crown, with arms numbered from dorsal (I) to ventral (IV) and stump of tentacle (between III and IV) (from Voss, 1963). 77, Sepiolinae, *Inioteuthis maculosa:* spread arm crown of male with hectocotylus (arm I); arrow indicating web covering tentacular base (from Voss, 1963).

REFERENCES.—Adam and Rees (1966), Guerra (1985), Mangold-Wirz (1963), Roeleveld (1972), Roeleveld and Liltved (1985), Roper et al. (1984), Roper and Hochberg (1988), Sasaki (1929).

Family SEPIADARIIDAE Naef, 1912

FAMILY CHARACTERS (Figure 71).—Shell absent; dorsal mantle margin fused to head; ventral mantle margin fused to funnel (no locking apparatus) (except in *Sepioloidea*); arm suckers in 2 rows proximally, 4 rows distally (except in *Sepiadarium gracilis* and *Sepioloidea pacifica,* which have 2 rows of suckers only).

GEOGRAPHICAL DISTRIBUTION.—*Sepiadarium* in Indo-Malayan and Australian regions; *Sepioloidea* restricted to Australia and New Zealand.

VERTICAL DISTRIBUTION.—Benthic; in coastal waters of less than 100 m.

REMARKS.—Adults are very small, ranging from 20 to 40 mm ML.

Key to Genera of SEPIADARIIDAE

Ventral mantle margin fused with base of funnel on either side; no cartilaginous articulations [Figure 71] . . . . . ***Sepiadarium***

Funnel locking-cartilage with two depressions, anterior one deepest and widest [Figure 75] . . . . . ***Sepioloidea***

REFERENCES.—Berry (1921, 1932), Dell (1952), Voss (1963), Voss and Williamson (1971).

Family SEPIOLIDAE Leach, 1817

FAMILY CHARACTERS.—Shell reduced to chitinous gladius or absent in *Euprymna* and *Stoloteuthis*?; mantle short, broad and sac-like; fins large, round, separated; mantle-funnel locking-cartilage simple, straight.

Key to Subfamilies of SEPIOLIDAE

1. Arms I, II, and III connected by deep web [Figure 76] . . . . . **HETEROTEUTHINAE**
   Only arms III and IV connected by deep web [Figure 77] 2
2. Anterior edge of dorsal mantle free . . . . . **ROSSIINAE**
   Anterior edge of dorsal mantle fused with head . . . . . **SEPIOLINAE**

REFERENCES—Boletzky (1971), Fioroni (1981), Roper et al. (1984).

Subfamily HETEROTEUTHINAE Appellof, 1898

GEOGRAPHICAL DISTRIBUTION.—Worldwide; temperate to tropical waters.

VERTICAL DISTRIBUTION.—*Heteroteuthis* is pelagic from a few meters to about 500 m, mostly 25–150 m. Other genera are poorly known, but probably are demersal or midwater dwellers.

REMARKS.—Adult size ranges from 20 to 40 mm ML; egg size is about 2 mm.

Key to Genera of HETEROTEUTHINAE

1. Dorsal mantle edge free 2
   Dorsal mantle edge fused with head 3
2. Anterior fin attachment posterior to dorsal midpoint of mantle [Figure 78] . . . . . ***Heteroteuthis***
   Anterior fin attachment anterior to dorsal midpoint of mantle [Figure 79] . . . . . ***Nectoteuthis***
3. Dorsal mantle margin separated from head by prominent fold or ridge [Figure 80] . . . . . ***Iridoteuthis***
   Dorsal mantle margin united with head by broad band 4
4. Indo-Pacific [Figure 81] . . . . . ***Sepiolina***
   Atlantic [Figure 82] . . . . . ***Stoloteuthis***

REFERENCES.—Berry (1911a, b), Boletzky (1978), Naef (1912a, b, 1923), Verrill (1882), Voss (1963).

Subfamily ROSSIINAE Appellof, 1898

GEOGRAPHICAL DISTRIBUTION.—*Rossia* in all oceans; *Semirossia* in the western Atlantic; *Neorossia* in the Mediterranean Sea and eastern Atlantic from Portugal southward to Gulf of Guinea.

VERTICAL DISTRIBUTION.—Nectobenthic, generally 50–600 m; *Rossia pacifica* occurs as shallow as 10 m.

REMARKS.—Adult size ranges from 50 to 80 mm ML; egg size ranges from 5 to 7 mm.

Key to Genera of ROSSIINAE

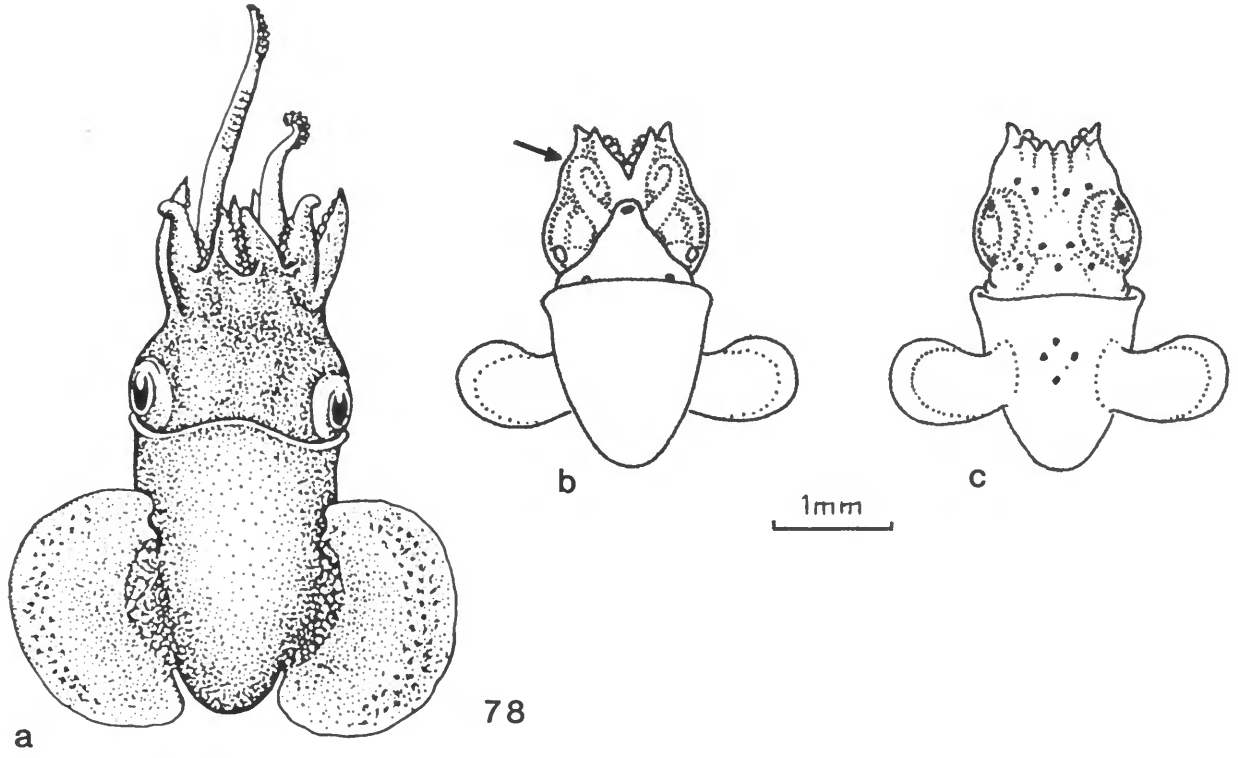
1. Light organs present on ink sac [Figure 83] . . . . . ***Semirossia***
   Light organs absent on ink sac 2
2. Ink sac functional; anal flaps well developed [Figures 84, 85] . . . . . ***Rossia***
   Ink sac nonfunctional; anal flaps very poorly developed [Figures 86, 87] . . . . . ***Neorossia***

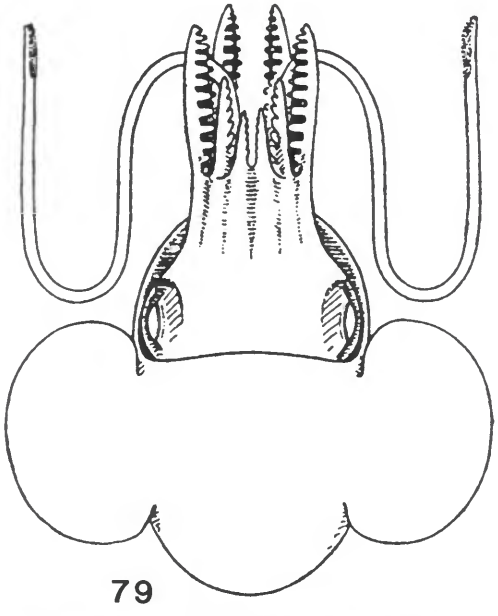
REFERENCES.—Boletzky (1970, 1971), Boletzky and Boletzky (1973), Guerra (1982a), Sasaki (1929), Summers (1985a, b), Voss (1956).

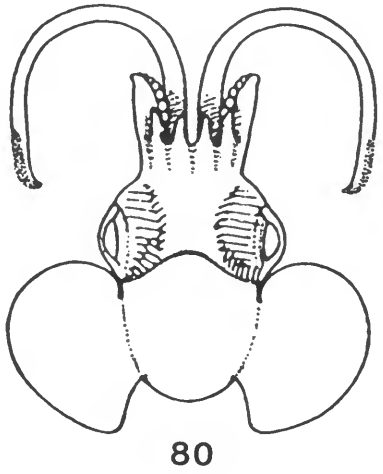
Subfamily SEPIOLINAE Appellof, 1898

GEOGRAPHICAL DISTRIBUTION.—Worldwide; temperate to tropical waters.

VERTICAL DISTRIBUTION.—Nectobenthic, in very shallow

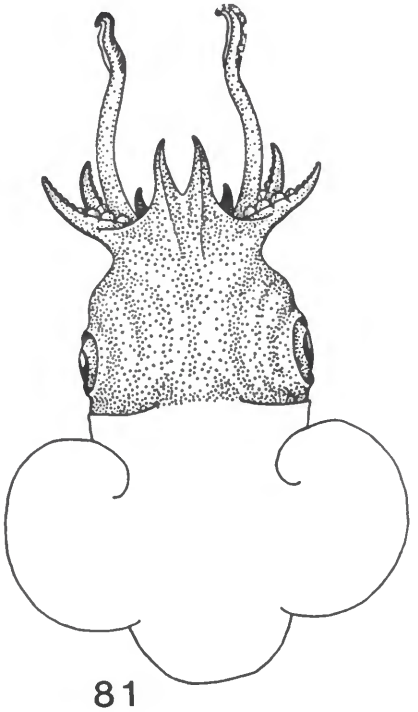






FIGURES 78–80 (above).—78, *Heteroteuthis: a, H. hawaiiensis:* dorsal view of adult (from Berry, 1914); *b,c:* views of very young *H. dispar: b,* ventral; *c,* dorsal; arrow pointing at curled tentacles (from Naef, 1923). 79, *Nectoteuthis pourtalesi:* dorsal view of adult (from Naef, 1923). 80, *Iridoteuthis iris:* dorsal view of adult (from Naef, 1923).

FIGURES 81–83 (oposite page).—81, *Sepiolina nipponensis:* dorsal view of adult (from Voss, 1963). 82, *Stoloteuthis leucoptera:* dorsal view of adult (Vecchione, unpublished). 83, *Semirossia tenera: a,* dorsal view of adult (from Verrill, 1881); *b,* ventral view of visceral mass with light organ (lo), papilla of light organ (lp), kidney papilla (kp), vena cephalica (vc); arrows point at well-developed anal flaps (cf. Figure 87) (from Boletzky, 1971).



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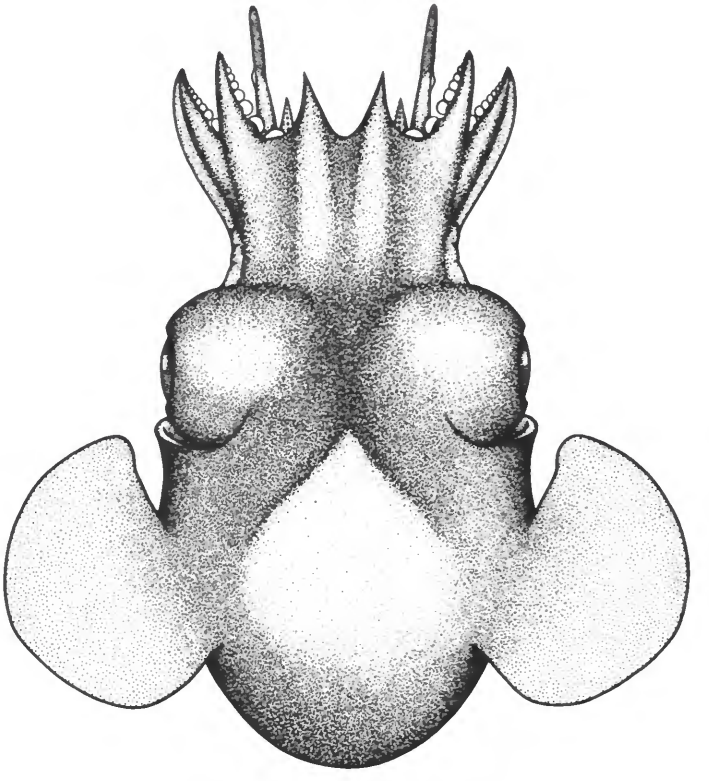

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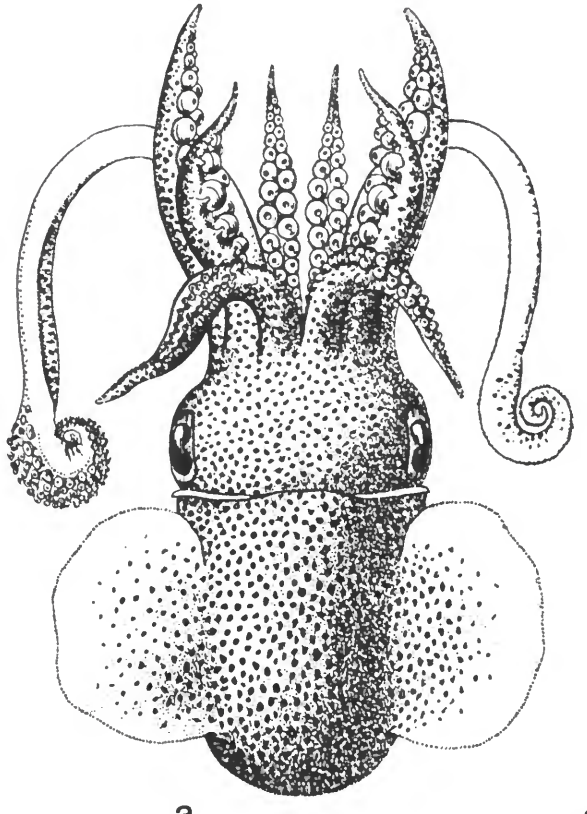

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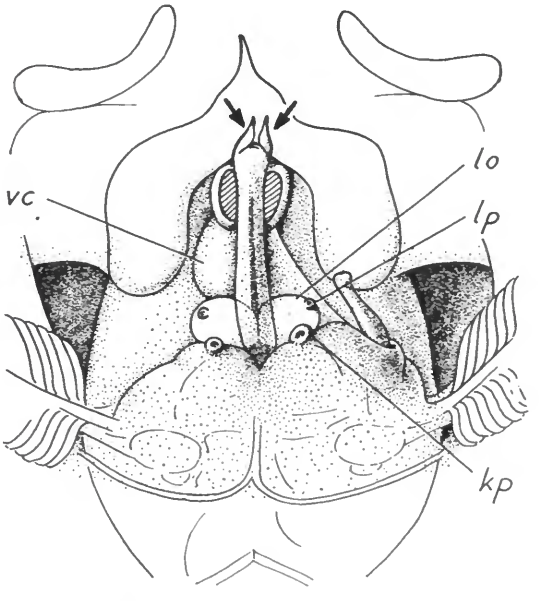

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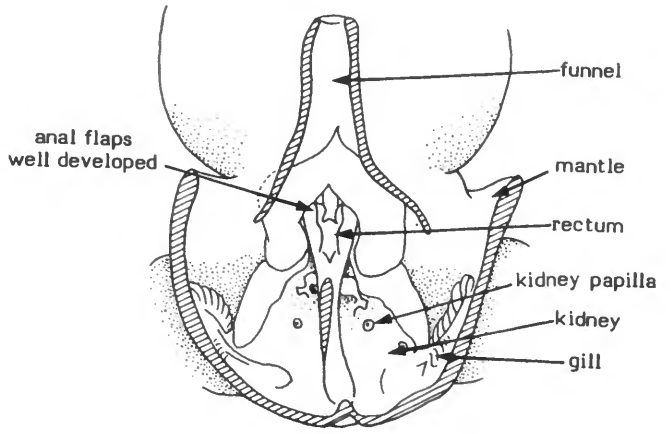

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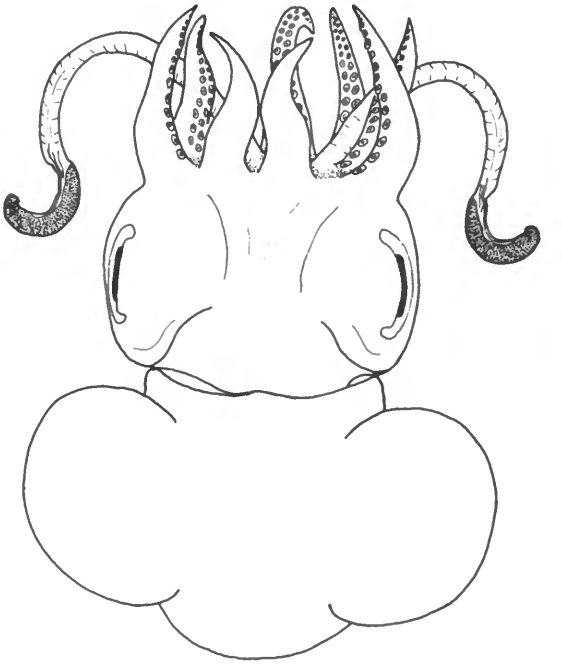

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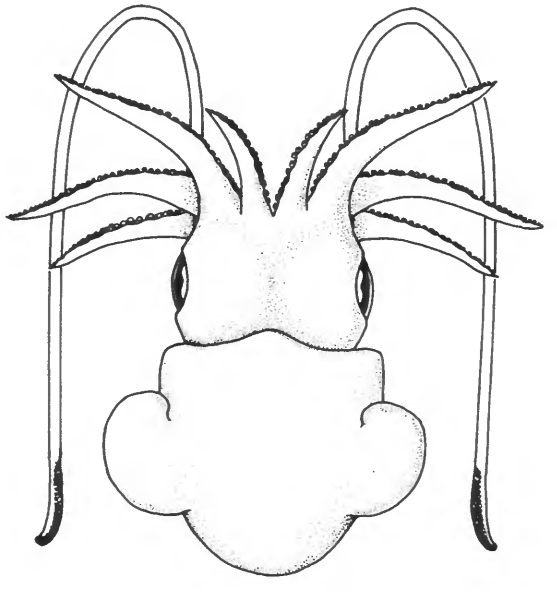

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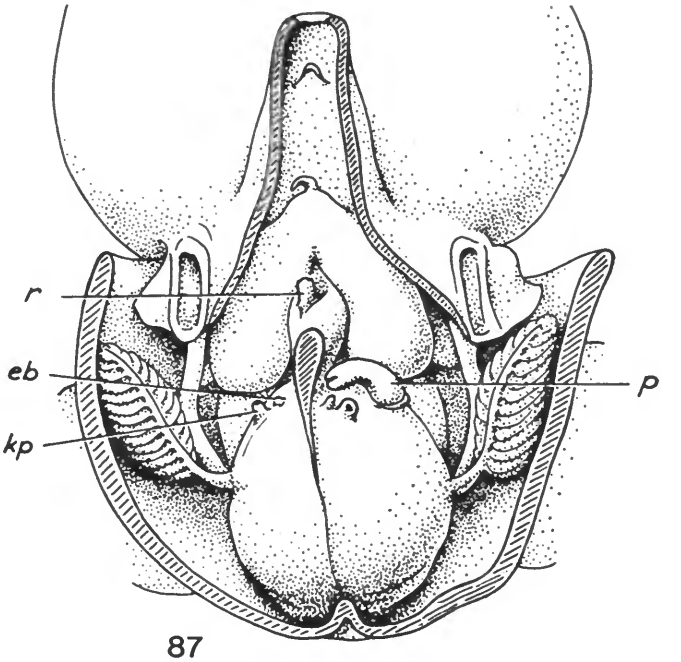
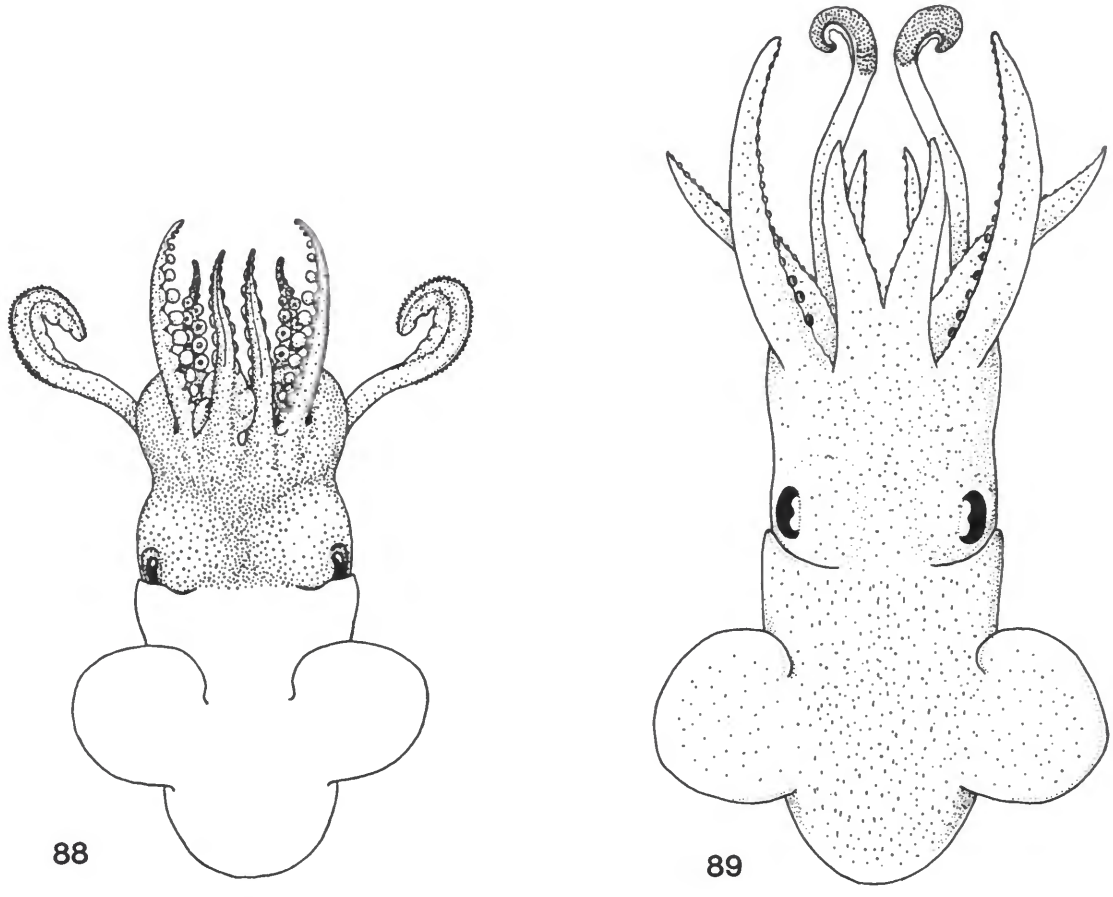


87

FIGURES 84–87.—84, *Rossia* sp: ventral view of visceral mass. 85, *Rossia antillensis:* dorsal view of adult (from Roper et al., 1984). 86, *Neorossia caroli:* dorsal view of adult (from Roper et al., 1984). 87, *Neorossia* sp.: ventral view of visceral mass of male with penis (p), kidney papillae (kp), epirenal bodies (eb), rectum (r); note absence of anal flaps (cf. Figure 83*b*) (from Boletzky, 1971).



FIGURES 88, 89.—88, *Sepietta oweniana:* dorsal view of adult (from Roper, et al., 1984). 89, *Inioteuthis maculosa:* dorsal view of adult (from Voss, 1963).

waters to several hundred meters on the continental shelf and slope.

REMARKS.—Adult size ranges from 20 to 50 mm ML; egg size ranges from 1.5 to 4 mm.

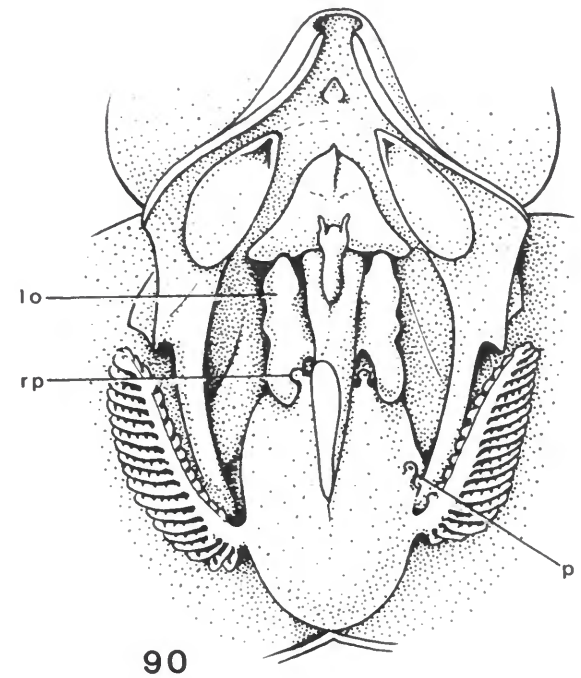
Key to Genera of SEPIOLINAE

1. No light organ on ink sac 2
   Light organ on ink sac 3
2. Suckers on tentacular club in 16–32 rows [Figure 88] . . . . . ***Sepietta***
   Suckers on tentacular club in 8–10 rows [Figure 89] . . . . . ***Inioteuthis***
3. Tentacular club with more than 16 sucker rows; light organ on ink sac saddle-shape with lateral components (lenses) roughly parallel [Figures 90, 91] . . ***Euprymna***
   Tentacular club with up to 16 sucker rows; light organ on ink sac more or less bilobed, nonparallel 4
4. Light organ on ink sac kidney bean-shape on each side [Figures 92, 93] . . . . . ***Sepiola***
   Light organ on ink sac bilobed only in young, becoming compact, lens-shape in adults [Figures 94, 95] . . . . . ***Rondeletiola***

REFERENCES.—Boletzky et al. (1971), Guerra (1982b, 1985), Herring et al. (1981), Mangold-Wirz (1963), Naef (1923), Voss (1963).

Family IDIOSEPIIDAE Appellof, 1898

FAMILY CHARACTERS.—Gladius chitinous, very delicate, shorter than mantle; body elongate; dorsal mantle margin free. Monogeneric.



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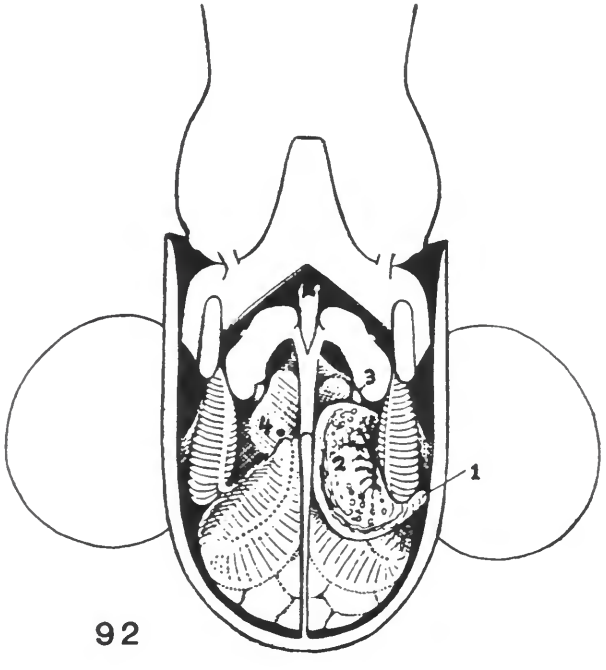

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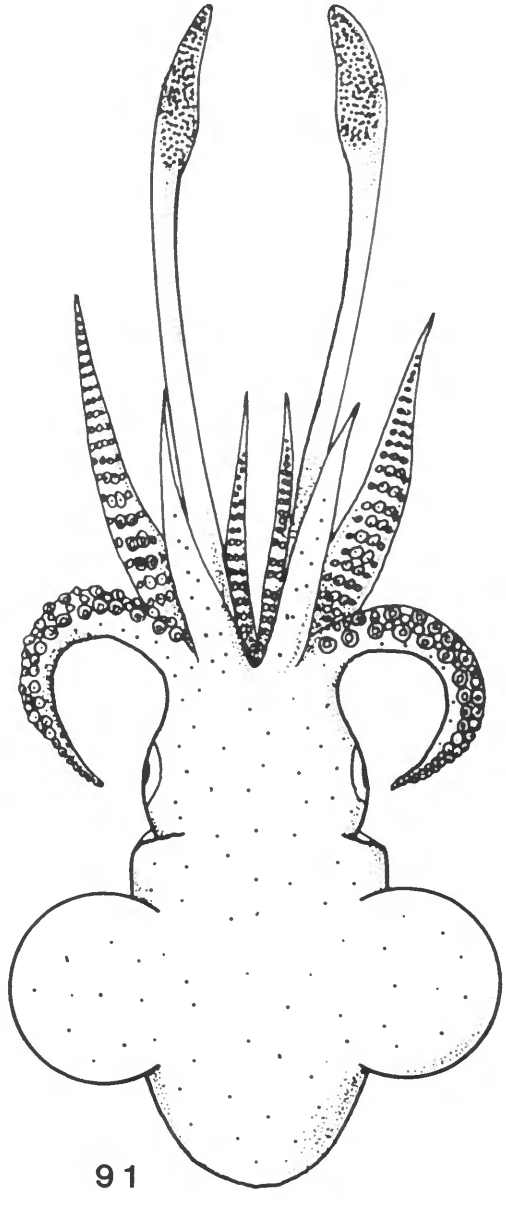

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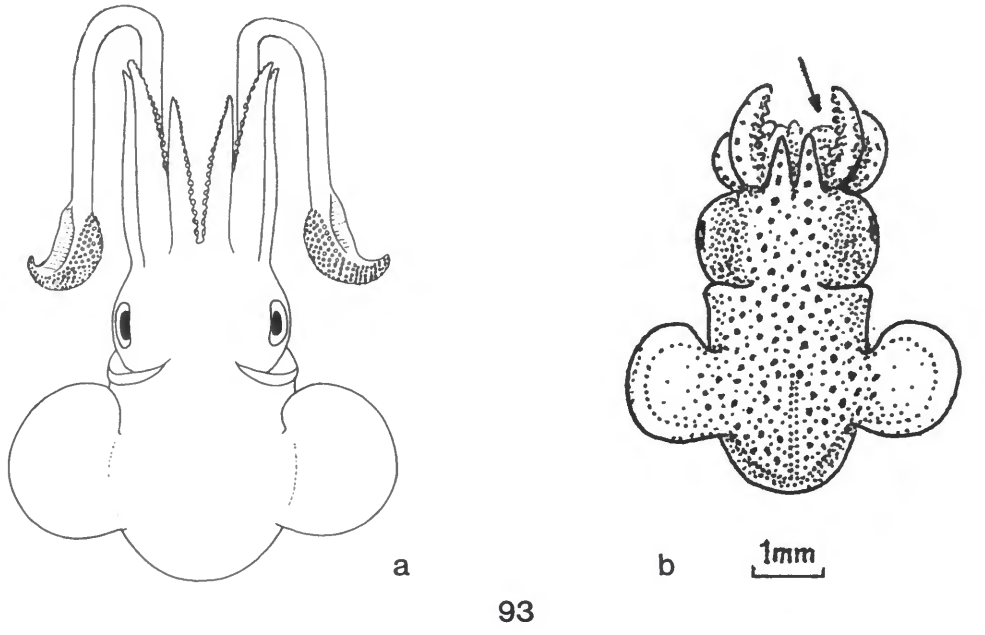
FIGURES 90-92.—90, *Euprymna berryi:* ventral view of visceral mass of male with light organ (lo), renal papilla (rp), penis (p) (from Sasaki, 1929). 91, *Euprymna morsei:* dorsal view of adult (from Roper et al., 1984). 92, *Sepiola affinis:* ventral view of visceral mass of adult female with bursa copulatrix (1,2), renal papillae (3), lying on either side of accessory nidamental glands (4) (from Naef, 1923).



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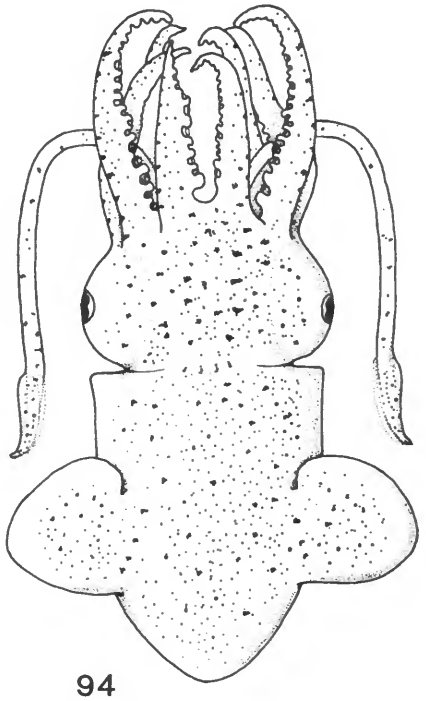

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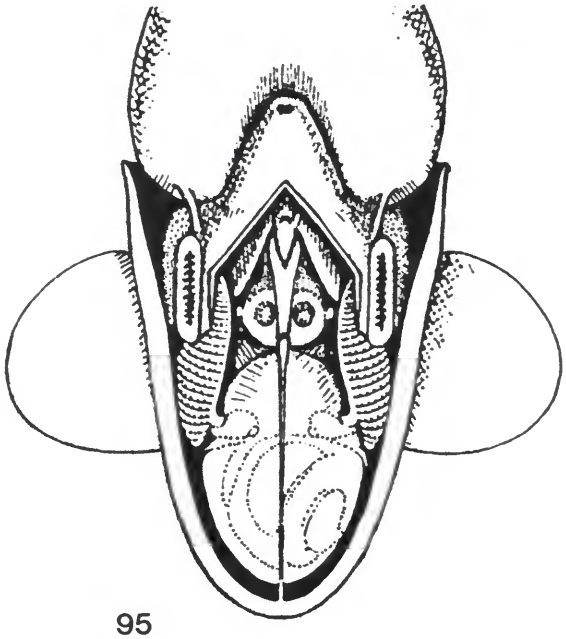

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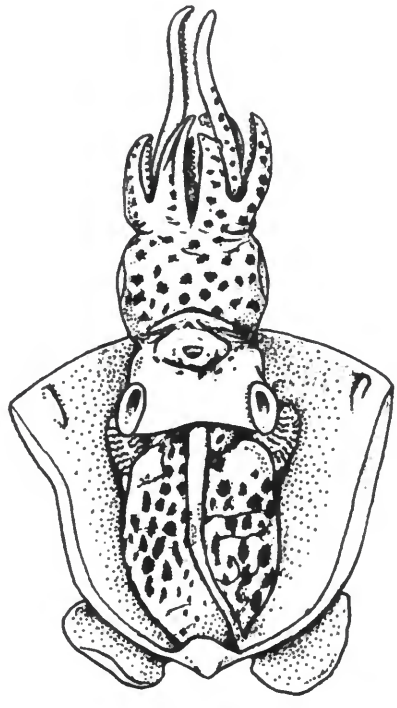
FIGURES 93-95.—93, *Sepiola* sp.: *a*, general aspect of adult with tentacles in *post mortem* condition; *b*, hatchling with tentacles curled (arrow) as in living and freshly fixed specimens (Boletzky, unpublished). 94, *Rondeletiola* sp.: dorsal view of adult (from Roper et al., 1984). 95, *Rondeletiola minor:* ventral view of visceral mass of adult male (from Naef, 1923).



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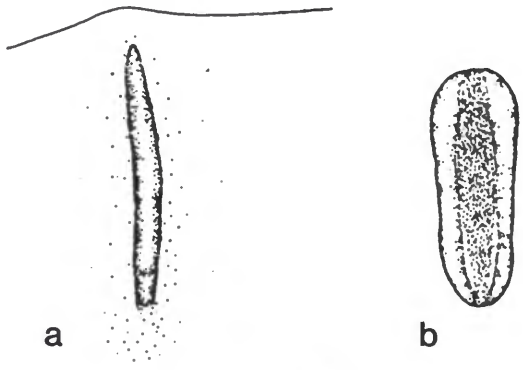

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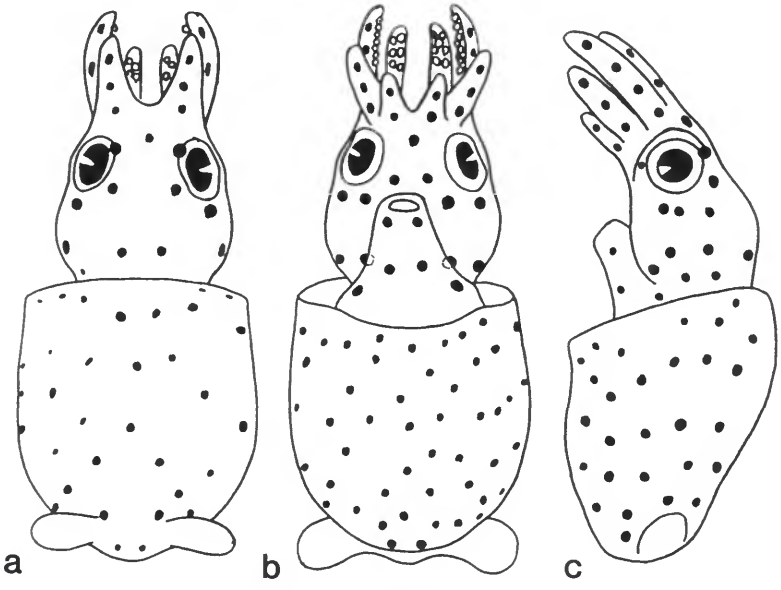

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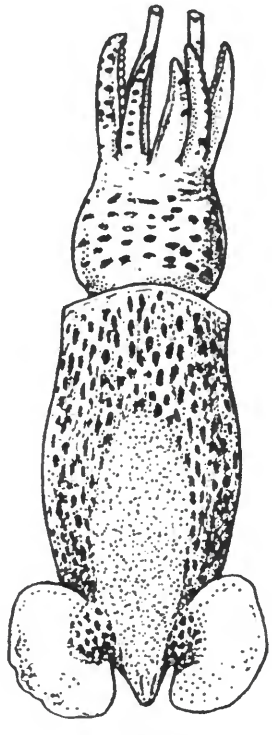

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FIGURES 96–99.—96, *Idiosepius paradoxus:* ventral view of visceral mass (from Sasaki, 1929). 97, *Idiosepius notoides,* mantle-funnel locking-cartilages components: *a,* mantle; *b,* funnel (Lu, unpublished). 98, 99, *Idiosepius paradoxus:* 98, Views of hatchling, 1 mm ML: *a,* dorsal; *b,* ventral; *c,* lateral (from Natsukari, 1970). 99, Dorsal view of adult (from Sasaki, 1929).

Idiosepius Steenstrup, 1881

GENERIC CHARACTERS (Figures 96–99).—With characters of the family. Locking-cartilage deep, oval-shape in *Idiosepius pygmaeus* or simple, straight in *I. notoides* [Figures 97].

GEOGRAPHICAL DISTRIBUTION.—Japan to Australia; South Africa; not known from Atlantic.

VERTICAL DISTRIBUTION.—Sublittoral in coastal sea grass beds.

REFERENCES.—Berry (1921, 1932), Voss (1963).

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Order TEUTHOIDEA Naef, 1916

ORDINAL CHARACTERS.—Ten circumoral appendages, tentacles contractile, but not retractile into pockets (occasionally tentacles secondarily lost); suckers with chitinous rings and/or hooks. Radular teeth commonly with primary projection and secondary cusp(s), especially on the median (rachidian) and the first lateral teeth; buccal membrane present. Olfactory organ consists of two projecting papillae without protective epithelium; eye (1) covered with a transparent membrane, with a minute pore (Myopsida), or (2) completely open to the sea (Oegopsida). Gills with branchial canal between afferent and efferent branchial blood vessels. Digestive gland a single structure. Shell internal, a simple, rod-like or feather-like, chitinous gladius.

Suborder MYOPSIDA Orbigny, 1845

(by R.T. Hanlon, S. v. Boletzky;
T. Okutani, G. Perez-Gandaras, P. Sanchez,
C. Sousa-Reis, and M. Vecchione*)

SUBORDINAL CHARACTERS.—Corneal membrane covers eye, with minute pore anteriorly; suckers of arms and clubs never modified as hooks; suckers may be present on buccal lappets; female with accessory nidamental glands and single gonoduct.

REMARKS.—The taxa are arranged by geographical locale, based on early life stages, and distributions are limited to continental shelf areas.

Family PICKFORDIATEUTHIDAE Voss, 1953

FAMILY CHARACTERS.— *Adults* (Figure 101): Two rows of suckers on manus of tentacular club; arm suckers biserial; fins separate, small, round with convex posterior borders; buccal membrane with reduced lappets and no suckers; photophores absent.

GEOGRAPHICAL DISTRIBUTION.—Subtropical to tropical western North Atlantic, Caribbean, and Gulf of Mexico.

VERTICAL DISTRIBUTION.—Very shallow water; associated with sea grass beds.

REMARKS.—Adults are very small (13–40 mm ML). Juvenile characters were not examined, but are likely to be similar to other loliginids. One or more undescribed species is known to exist.

REFERENCES.—Hess (1987), Voss (1953, 1956).

Family LOLIGINIDAE Steenstrup, 1861

FAMILY CHARACTERS.— *Adults*: Four rows of suckers on manus of tentacular club; arm suckers biserial; body fusiform of variable shape; fins united posteriorly, terminal-lateral; buccal membrane with 7 lappets usually set with small suckers; photophores occur rarely.

Young: Body form of hatchlings always bullet-shape with well-developed terminal fins; well-developed ventral arms (arms IV >I) and tentacles.

Eggs: Enclosed serially in gelatinous capsules and attached to substrate (Figure 100).

GEOGRAPHICAL DISTRIBUTION.—Worldwide except polar regions.

VERTICAL DISTRIBUTION.—Limited to neritic waters.

REMARKS.—Many species are of commercial value. Adult size ranges from 50 to 900 mm ML. Generally no great change in body form occurs between hatching and adults. The most conspicuous external changes are positive allometry in fin growth and distinctive chromatophore patterns in some adult forms (e.g., *Loligo plei*; see Hanlon, 1982). Extensive gaps in knowledge exist, especially in the young stages of *Uroteuthis*, *Loliolus*, and *Loliolopsis*. Little information is available from South America, Africa, and most of the Indo-Pacific. Young forms of *Loligo*, *Alloteuthis*, and *Doryteuthis* are so similar both between and within genera that it is usually impossible to distinguish species from preserved specimens.

Key to Genera of LOLIGINIDAE (Adults and Subadults)

(Adapted from Roper et al., 1984)

1. Mantle elongate or short, robust, posteriorly pointed or rounded, but never produced into an elongate, pointed tail; posterior border of fins straight, or only slightly concave, or rounded 2
   Mantle very long, narrow, its posterior end drawn out into a long, pointed tail, especially in males; posterior border of fins strongly concave, extending along tail as narrow membranes [Figure 108] 7
2. Fins very long (>90% ML), broad, *Sepia*-like, but much wider and more muscular; mantle very robust [Figure 102] . . . . . ***Sepioteuthis***
   Fins short to moderately long (<90% ML); mantle elongate and narrow to short and stocky 3
3. Fins lateral, rhombic in outline, with posterior borders straight or slightly concave; relatively long (usually >60% ML); mantle elongate, bluntly to sharply pointed [Figure 103*b*]; left ventral arm (IV) hectocotylized in males . . . . . ***Loligo*** and 4
   Fins terminal, rounded, with posterior borders convex, short (<60% ML); one or both ventral arms (IV) hectocotylized in males 5
4. Vane of gladius broad, with thin, curved edges [Figure 103*a*]; posterior end of mantle moderately blunt [Figure 103*b*]; mantle only moderately narrow in males; fins usually <70% ML . . . . . Subgenus ***Loligo****
   Vane of gladius narrow, thickened straight edges [Figure 104*a*]; posterior end of mantle relatively sharply pointed [Figure 104*b*]; mantle very narrow in males; fins usually >70% ML . . . . . Subgenus ***Doryteuthis****

*Junior authors listed alphabetically.

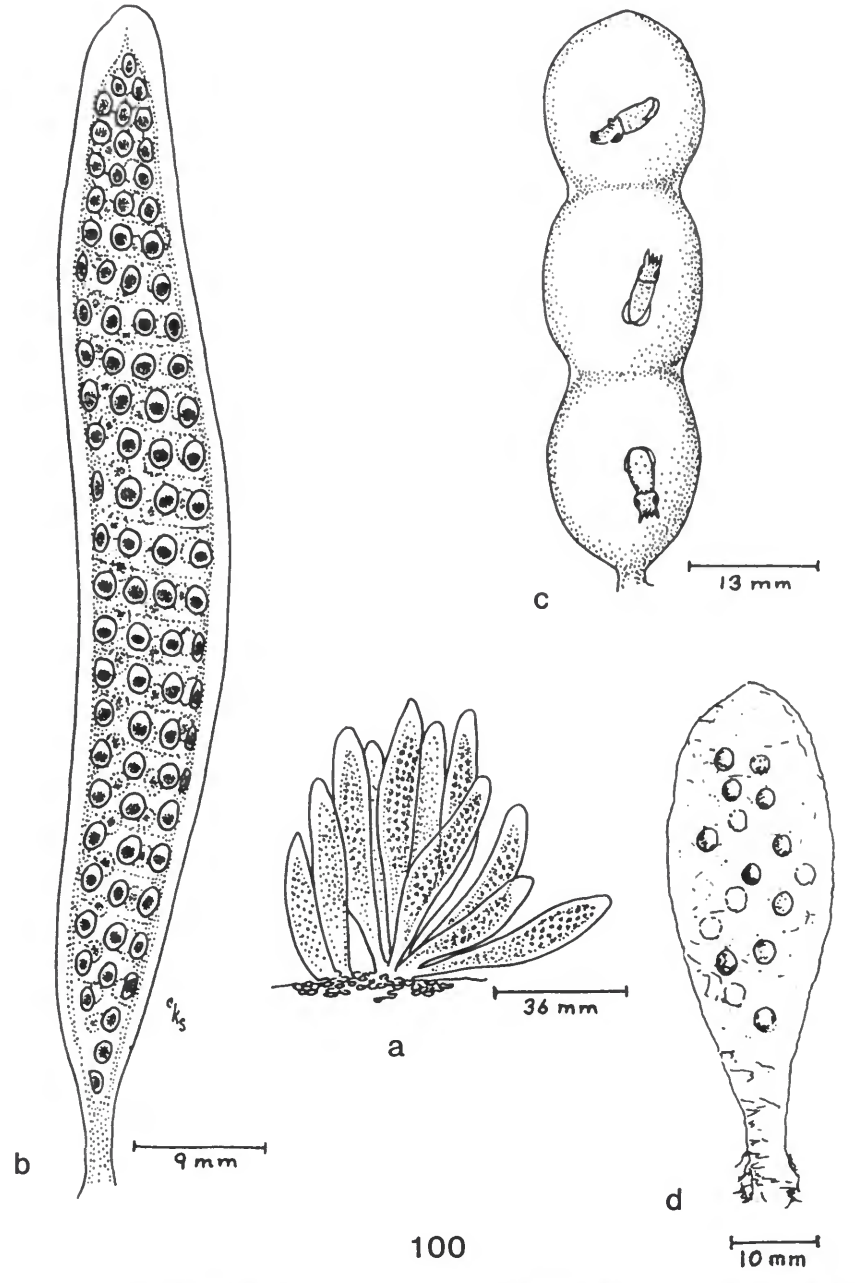
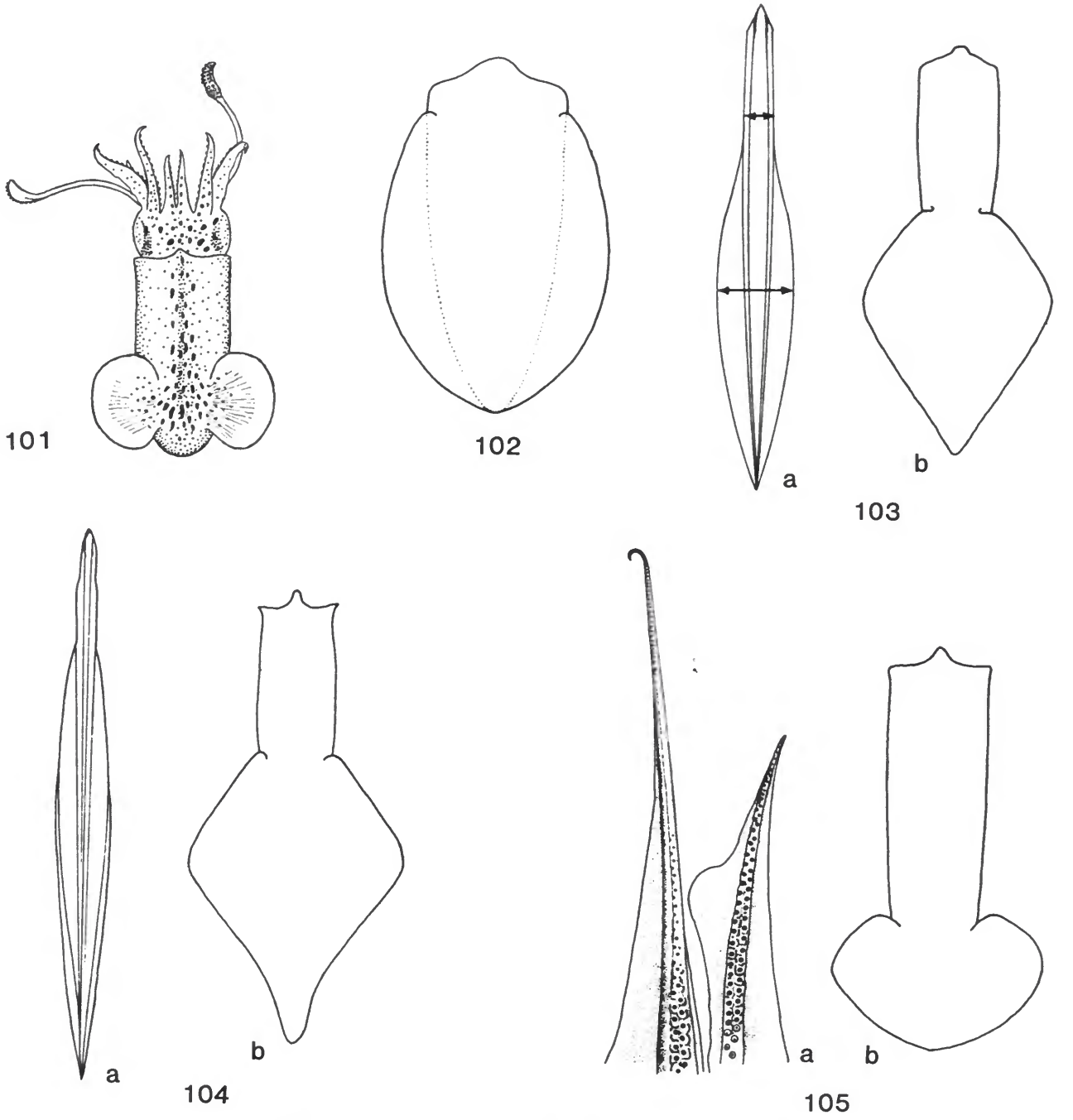


FIGURE 100.—Egg capsules of loliginid squids: *a*, *Loligo* (*Doryteuthis*) *plei*; *b*, *L. plei* with typical spiral arrangement of eggs within nidamental jellies; *c*, *Sepioteuthis sepioidea*, characterized by small number of large eggs per capsule, here shown at end of embryonic development with strongly extended envelope (from Roper, 1965); *d*, *Alloteuthis* sp. (after Jatta, 1896).



FIGURES 101–105.—101, *Pickfordiateuthis pulchella:* dorsal view, 22 mm ML, adult, Florida Keys (from Voss, 1953). 102, *Sepioteuthis* sp: dorsal view of mantle and fins. 103, *Loligo* (*Loligo*) sp: *a*, gladius; *b*, dorsal view of mantle and fins. 104, *Loligo* (*Doryteuthis*) sp: *a*, gladius; *b*, dorsal view of mantle and fins. 105, *Loliolopsis* sp: *a*, both arms IV of male hectocotylized; *b*, dorsal view of mantle and fins (102–105 from Roper et al., 1984).

5. One ventral arm (left IV) hectocotylized in males; mantle stout, rounded posteriorly; fins ≥50% ML (slightly less in smaller *Lolliguncula*) 6
   Both ventral arms (IV) conspicuously hectocotylized in males [Figure 105*a*]; mantle elongate, narrow, bluntly pointed posteriorly; fins 30% to 35% ML; elliptical to heart-shape [Figure 105*b*] . . . . . ***Loliolopsis***
6. 50% or less of ventral left arm (IV) hectocotylized by modification of suckers [Figure 106*a*]; fins round to elliptical; mantle very robust, muscular, bluntly rounded posteriorly; animals relatively large [Figure 106*b*] . . . . . ***Lolliguncula***
   Nearly entire length of left ventral arm (IV) hectocotylized by drastic modification of suckers, membranes, and trabeculae [Figure 107*a*]; fins elliptical to broadly heart-shape; mantle thin-walled, wide, broadly rounded posteriorly; animals relatively small [Figure 107*b*] . . . . . ***Loliolus***
7. Buccal membrane with suckers; trabeculae on protective membranes of tentacular clubs equal in number to adjacent suckers [Figure 109*a*] . . . . . ***Uroteuthis***
   Buccal membrane without suckers; trabeculae on protective membranes of tentacular clubs twice as numerous as adjacent suckers [Figure 109*b*] . . . . . ***Alloteuthis***

*The subgenera *Loligo* and *Doryteuthis* are considered valid genera by some authors. Further research is required to clarify their status.

WESTERN NORTH ATLANTIC LOLIGINIDAE

Sepioteuthis sepioidea (Blainville, 1823)

SPECIES CHARACTERS.—*Adults* (Figure 110*a,b*): Fins very long, >90% ML.

Young (Figure 110*c*): Hatchlings very large (5.0 mm ML); fins lobate, subterminal, grow anteriorly; chromatophores very dense over entire body except funnel.

GEOGRAPHICAL DISTRIBUTION.—Tropical western North Atlantic, northern Florida throughout Caribbean to Venezuela.

VERTICAL DISTRIBUTION.—Associated with coral reefs and grass flats; 0–20 m.

Lolliguncula brevis (Blainville, 1823)

SPECIES CHARACTERS.—*Adults* (Figure 111*a*): Fins terminal, rounded, and short (50%–55% ML); wider than long; mantle stout and bluntly rounded posteriorly.

Young (Figure 111*b–d*): Hatchlings 1.8 mm ML; despite small hatchling size, all 4 arms present at hatching; ventral head chromatophores arranged in triangle posterior to each eye from hatching to 8 mm ML (McConathy et al., 1980; Vecchione, 1982); no dark chromatophores on dorsal surface in hatchlings and always fewer chromatophores dorsally than *Loligo* of comparable size (Vecchione, 1982).

GEOGRAPHICAL DISTRIBUTION.—Western Atlantic (40°N–23°S).

VERTICAL DISTRIBUTION.—Neritic, coastal, 0–20 m.

Loligo spp. (*L. pealei, L. plei, L. roperi, L. ocula*)

SPECIES CHARACTERS.—*Adults* (Figure 112*a*): Fins longer than broad, usually 60% ML; body long, fusiform.

Young (Figure 112*b–d*): Hatchlings 1.5 mm ML; arm I not present at hatching; ventral head chromatophores arranged in roughly diamond-shape quadrangle posterior to each eye from hatching to at least 8 mm ML; number of chromatophores decreases from ventral to dorsal side.

GEOGRAPHICAL DISTRIBUTION.—Western North Atlantic, 50°N (*L. pealei*) to 45°S (*L. sanpaulensis*).

VERTICAL DISTRIBUTION.—Neritic to 400 m.

REMARKS.—The young of *L. roperi* and *L. ocula* are unknown (species limited to Caribbean waters). In *L. pealei* and *L. plei*, preserved specimens are very difficult to distinguish. An extensive distributional overlap exists among these species (Cohen, 1976; Roper et al., 1984) except north of Cape Hatteras where *L. pealei* is much more common and abundant than *L. plei*. Morphometric changes during growth of young *L. pealei* are presented by Vecchione (1981).

EASTERN NORTH ATLANTIC AND MEDITERRANEAN LOLIGINIDAE

Loligo forbesi Steenstrup, 1856

SPECIES CHARACTERS.—*Adults:* Suckers on manus of tentacular club all of similar size (i.e., no greatly enlarged suckers); chitinous rings of arm suckers with 7–8 teeth; fin length 75% ML in largest specimens.

Young (Figure 113): Mean size of live hatchling 3.7 mm ML (range 3.5–4.1 mm); number of chromatophores decreases from ventral to dorsal side, but less pronounced than in western Atlantic *Loligo*.

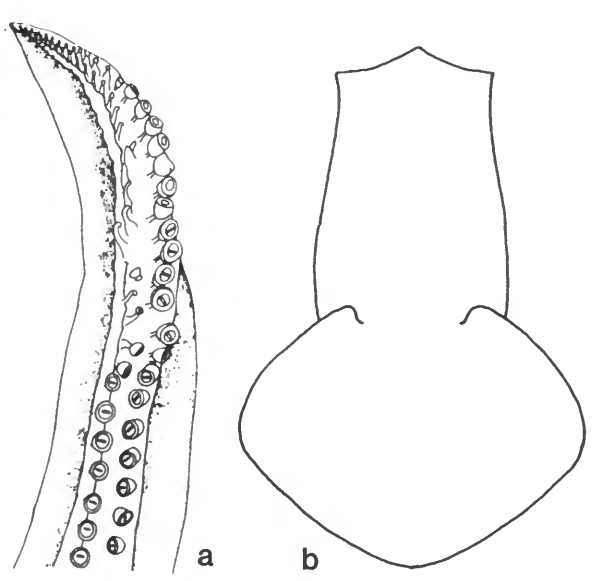
GEOGRAPHICAL DISTRIBUTION.—Eastern North Atlantic, 20°N–60°N; Mediterranean.

VERTICAL DISTRIBUTION.—Occurs from a few meters to 400 m.

Loligo vulgaris Lamarck, 1798

SPECIES CHARACTERS.—*Adults:* Suckers on median 2 rows of manus of tentacular club more than twice size of other suckers; chitinous rings of arm suckers with 20 teeth; fin length 65% ML in largest specimens.

Young (Figure 114): Mean size of live hatchling 3.1 mm ML (range 2.8–3.3 mm); chromatophore arrangement very similar to *L. forbesi* and just as variable.



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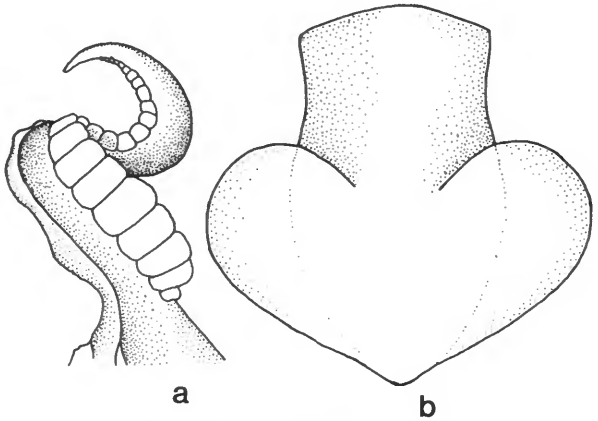

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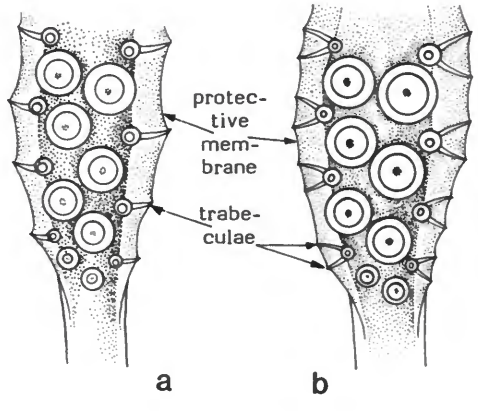


109

FIGURES 106–109.—106, *Lolliguncula* sp: *a*, hectocotylized arms IV of male; *b*, dorsal view of mantle and fins. 107, *Loliolus* sp: *a*, hectocotylized arms IV of male; *b*, dorsal view of mantle and fins. 108, *Uroteuthis bartschi:* dorsal view of mantle and fins. 109, Base of tentacular club: *a*, *Uroteuthis; b*, *Alloteuthis*. (From Roper et al., 1984.)

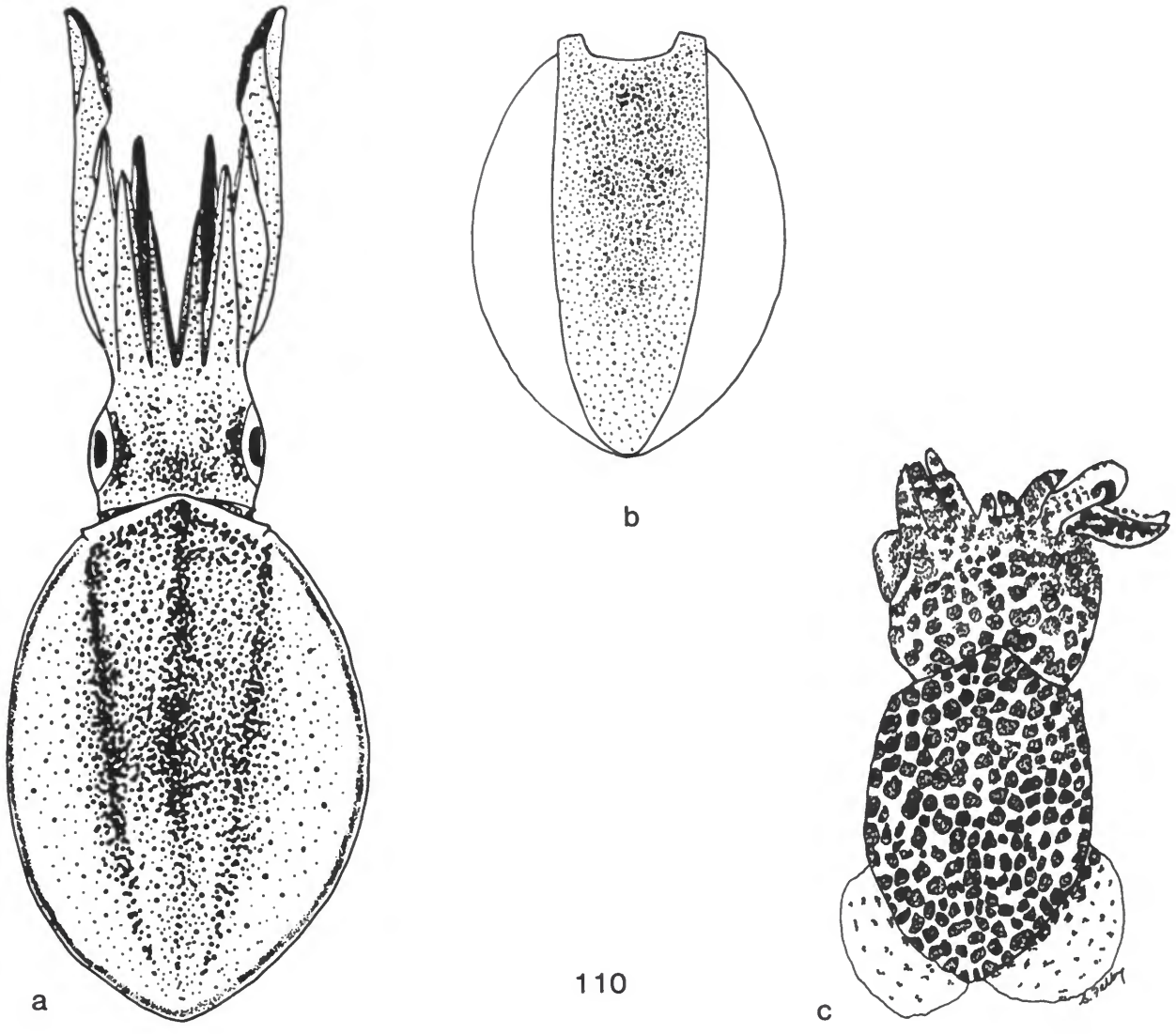


FIGURE 110.—*Sepioteuthis sepioidea: a,* dorsal view; *b,* ventral view of mantle and fins; *c,* living hatchling drawn from color slide (Hanlon, unpublished data).

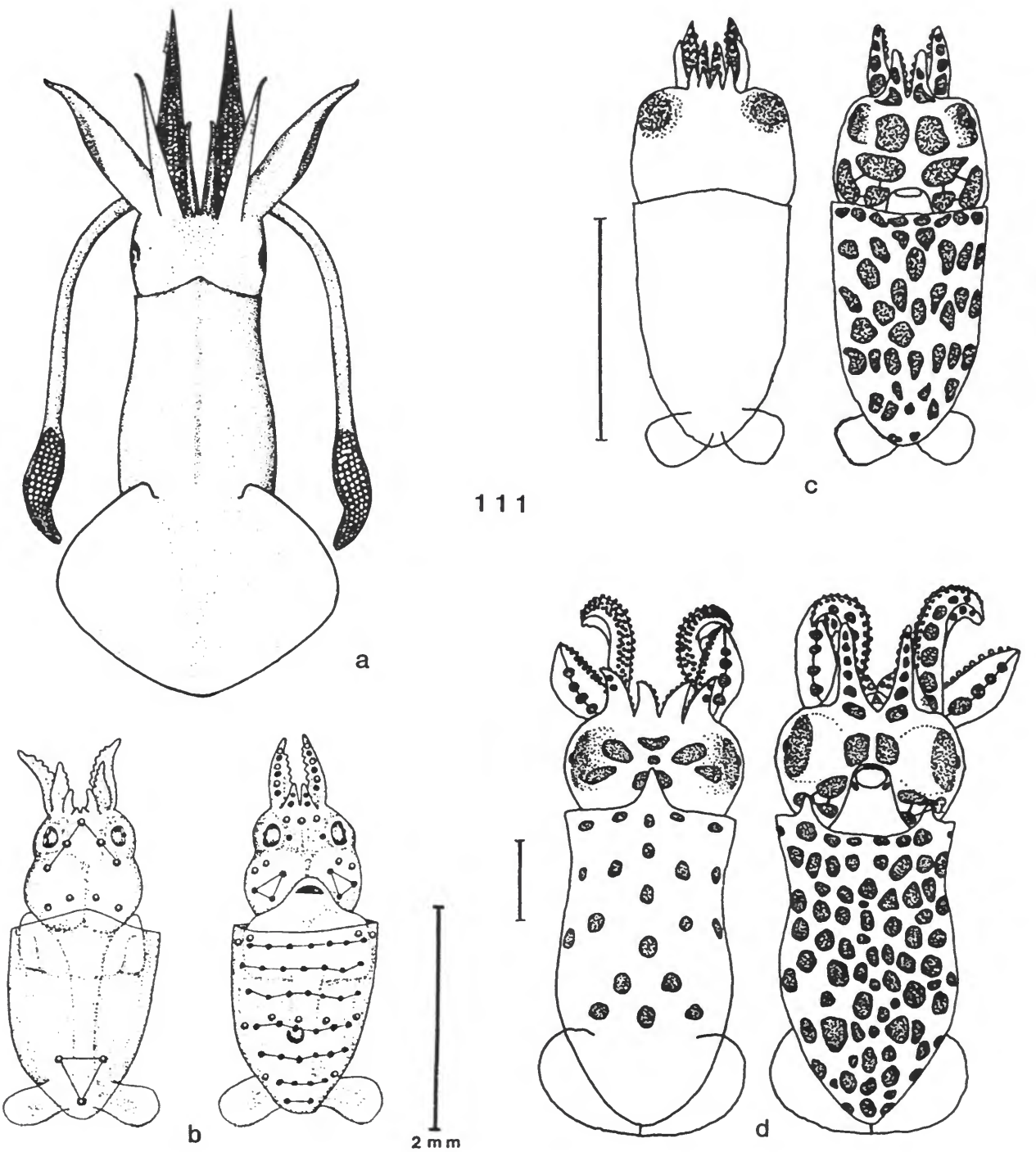


FIGURE 111.—*Lolliguncula brevis* (*b–d*, lines between chromatophores to show patterns): a, dorsal view of adult (from Roper et al., 1984); *b*, dorsal (left) and ventral views of live hatchling (closed circles red chromatophores, open circles yellow chromatophores) (from McConathy et al., 1980); *c,d*, preserved specimens of different sizes (same scale bar as *b*) in dorsal (left) and ventral views (from Vecchione, 1982).

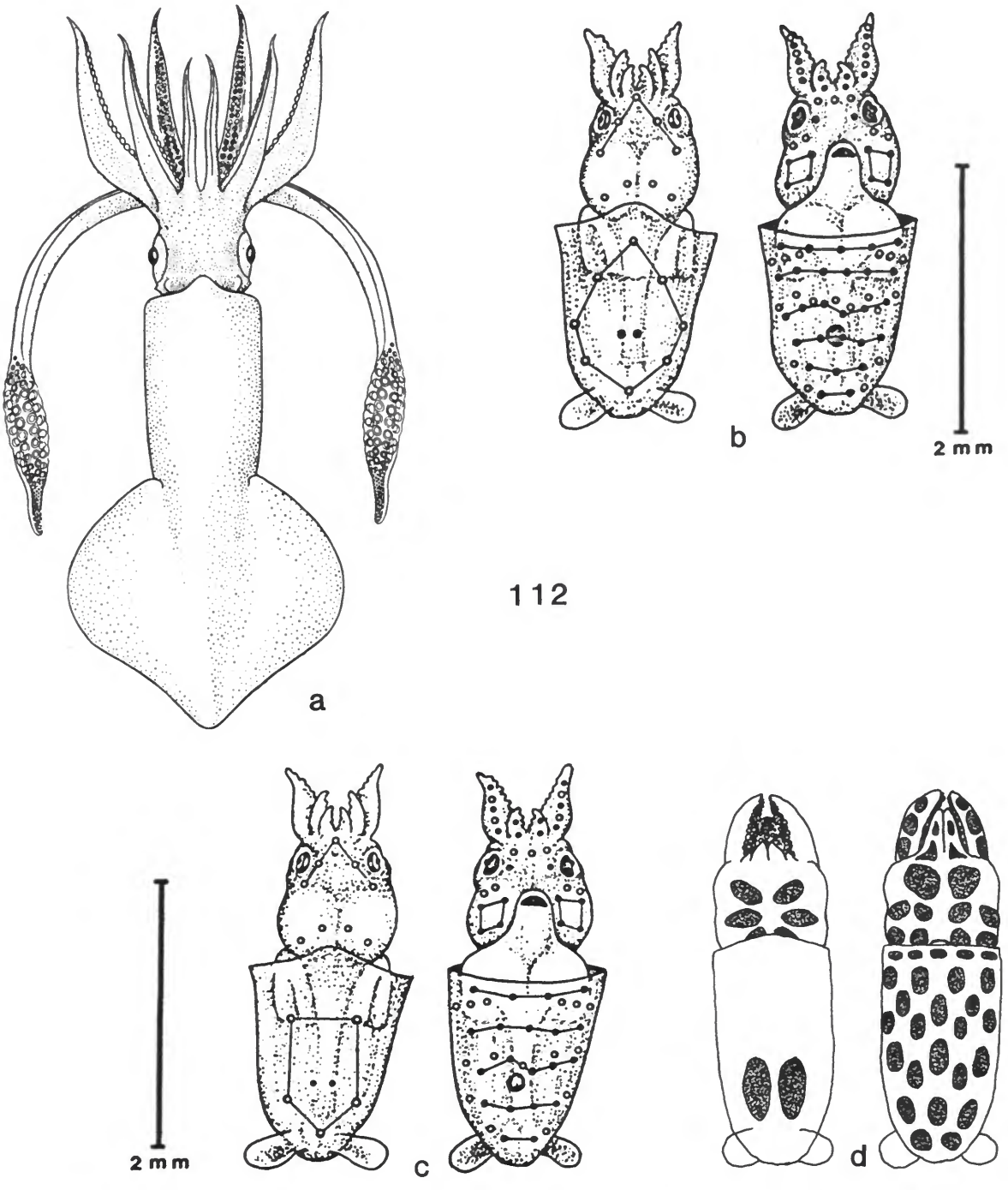
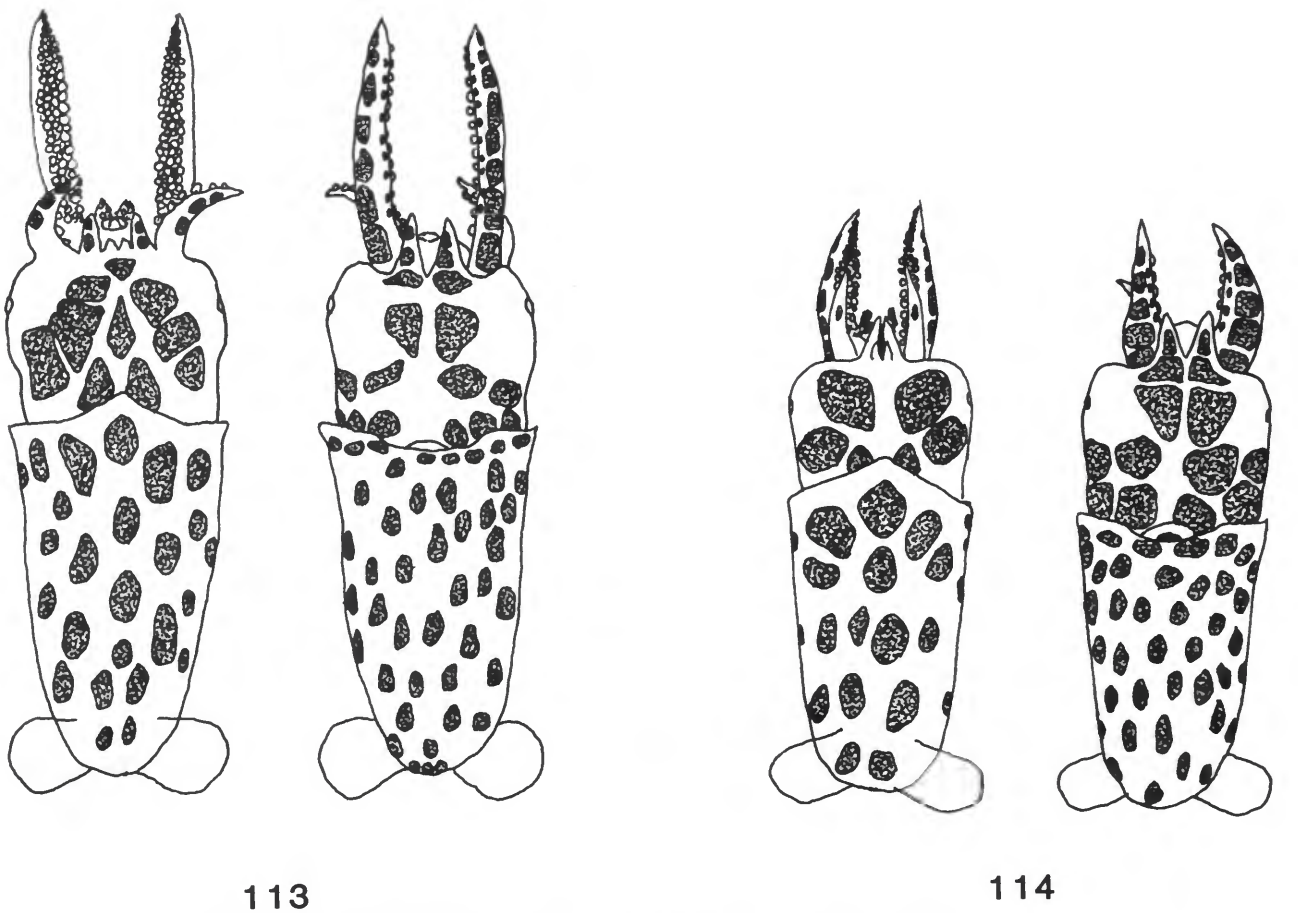


FIGURE 112.—*Loligo* spp: *a*, typical adult (from Roper et al., 1984), *b*, *L. pealei*, dorsal (left) and ventral views of live hatchlings (closed circles = red chromatophores, open circles = yellow chromatophores); *c*, *L. plei*, live hatchlings (*b,c*, from McConathy et al., 1980; lines between chromatophores to show patterns); *d*, *L. plei*, preserved hatchlings (original drawing).



FIGURES 113, 114.—Dorsal view (left) and ventral views of preserved hatchlings. 113, *Loligo forbesi*, 3.7 mm ML. 114, *Loligo vulgaris*, 3.1 mm ML. (Original drawings.)

GEOGRAPHICAL DISTRIBUTION.—Eastern Atlantic, 20°S-55°N; Mediterranean.

VERTICAL DISTRIBUTION.—From the surface to 200 m, possibly deeper.

Alloteuthis spp. (*A. media, A. subulata*)

SPECIES CHARACTERS.—*Adults* (Figure 115*a,b*): Mantle long, narrow, posterior end drawn into long tail, especially in males of *A. subulata;* no suckers on buccal membrane.

Young (Figure 115*c,d*): Very little known; hatchling approximately 2 mm ML; young stages nearly indistinguishable from *Loligo* spp.

GEOGRAPHICAL DISTRIBUTION.—*Alloteuthis media* is found around the British Isles and south into the Mediterranean. *Loligo forbesi, L. vulgaris,* and *Alloteuthis subulata* overlap south of the British Isles, with *L. forbesi* more common below 60 m. *A. subulata* and *L. vulgaris* co-occur only along the southern coast of England, while *L. forbesi* extends around the north of Scotland (Clarke, pers. comm.). All occur throughout the Mediterranean.

REMARKS.—These diagnoses apply to species north of Gibraltar and in the Mediterranean because the fauna of the Atlantic African coast is not well documented for young stages, e.g., *A. africana* (Allue et al., 1977; Guerra and Perez-Gandaras, 1983; Roper et al., 1984). Only *L. forbesi* occurs in the Azores (Martins, 1982) and it is more common in the British Isles (Holme, 1974) than *L. vulgaris.* Figure 116 illustrates size ranges of all four species (*L. forbesi, L. vulgaris, A. media,* and *A. subulata*).

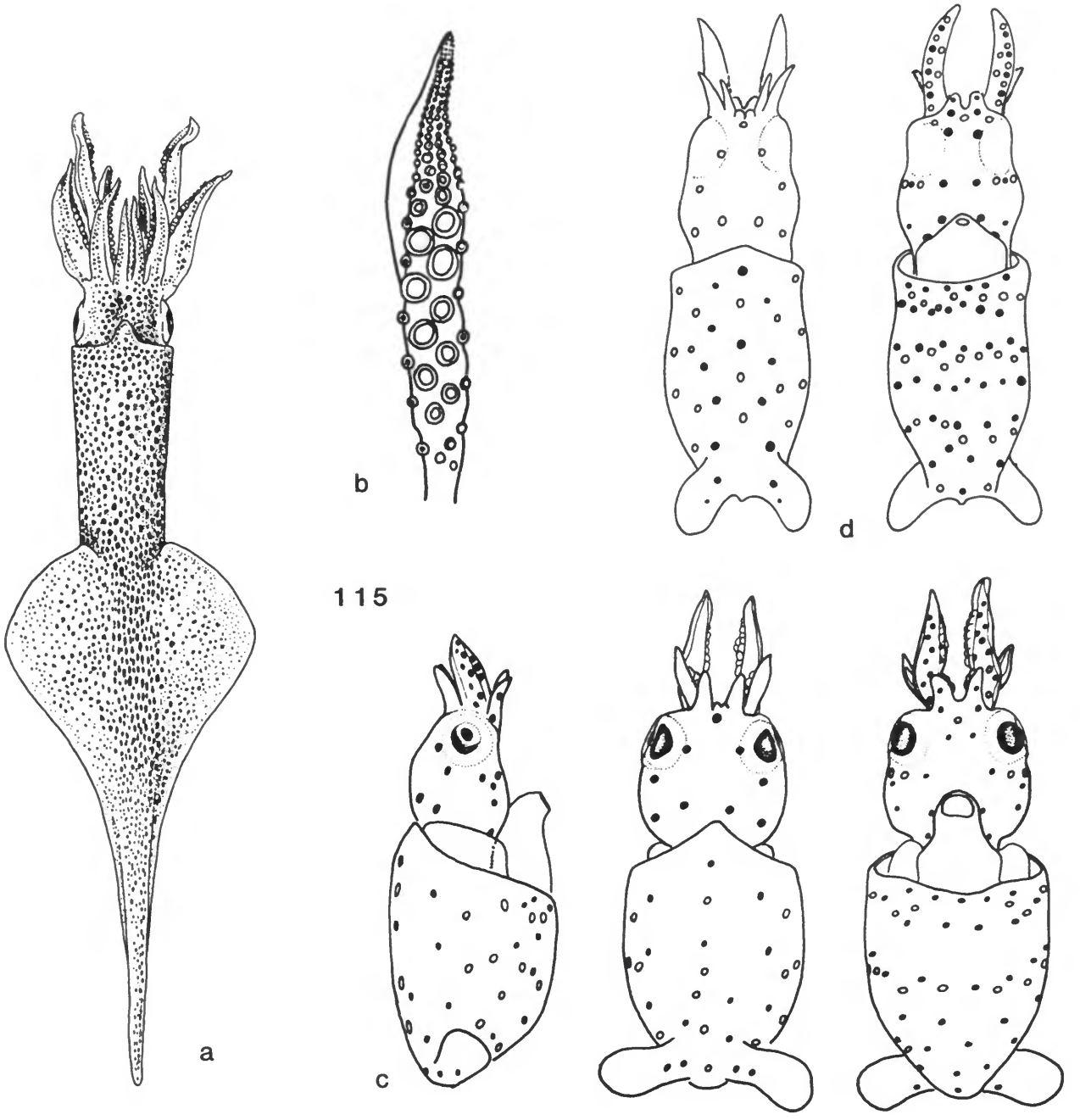


FIGURE 115.—*Alloteuthis* spp: *a*, dorsal view of typical adult male; *b*, tentacular club of adult; *c*, *A. subulata*, live hatchlings, 2 mm ML (closed circles = red chromatophores, open circles = yellow chromatophores) (C. Morris, unpublished); *d*, *A. media*, live hatchlings (from Fioroni, 1965).

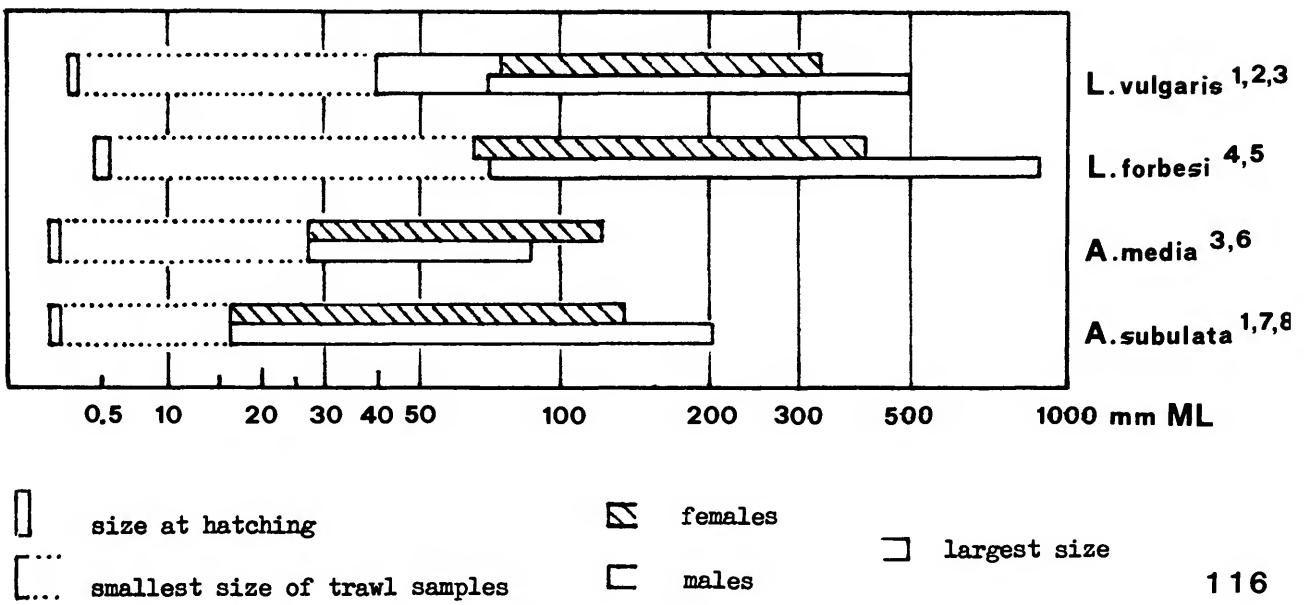


FIGURE 116.—Synopsis of hatchling and adult sizes of four eastern Atlantic loliginid species. References: 1, Perez-Gandaras (1983); 2, Worms (1977); 3, Mangold-Wirz (1963); 4, Holme (1974); 5, Rost (1981); 6, Fioroni (1982); 7, Adam (1952); 8, Morris (pers. comm.).

EASTERN NORTH PACIFIC AND HAWAIIAN LOLIGINIDAE

Sepioteuthis lessoniana Lesson, 1830

SPECIES CHARACTERS.—*Adults* (Figure 117*a,b*): Mantle long, robust; fin length 90%–100% ML, fin width up to 75% ML.

Young (Figure 117*c*): Hatchlings very large, approximately 10 mm ML; fins lobate, terminal, rapidly grow anteriorly; chromatophores very dense over entire body except funnel.

GEOGRAPHICAL DISTRIBUTION.—Indo-Pacific, easternmost limit Hawaii.

Loligo opalescens Berry, 1911

SPECIES CHARACTERS.—*Adults* (Figure 118*a,b*): Mantle slender; head and arms compact; arms short; tentacular clubs narrow; tentacular sucker rings with approximately 30 blunt teeth; arm sucker rings with 9–12 blunt teeth.

Young (Figure 118*c*): Hatchlings medium size, approximately 2.7 mm ML (large for North American species); dorsal chromatophores distinguish hatchlings of *L. opalescens* from juveniles of *Lolliguncula* present in eastern Pacific off Mexico and Central America.

GEOGRAPHICAL DISTRIBUTION.—Eastern North Pacific, 25°N–50°N.

REMARKS.—*L. opalescens* is the only loliginid found on the west coast of North America north of Mexico. From Mexico south, several loliginids overlap in distribution. No reports are known for early stages of these southern species, which include the genera *Loliolopsis* and *Lolliguncula* (Brakoniecki, 1980). *Sepioteuthis lessoniana* is the only loliginid known from the Hawaiian Islands (Berry, 1911; Roper et al., 1984).

WESTERN PACIFIC AND JAPANESE LOLIGINIDAE

Sepioteuthis lessoniana Lesson, 1830

REMARKS.—See Eastern North Pacific and Hawaiian Loliginidae.

Loligo edulis Hoyle, 1885

SPECIES CHARACTERS.—*Adults* (Figure 119): Mantle elongate, muscular; fin length about 70% ML with shallow, concave posterior margin; arm sucker rings with 8–10 high, blunt teeth on distal margin; large tentacular suckers, same size as largest suckers of arm III, with 30–40 sharply pointed, conical teeth; fusiform bilobed light organ on ink sac.

Young: No information available.

GEOGRAPHICAL DISTRIBUTION.—Western Pacific, Japan to northern Australia.

REMARKS.—The western Japan Sea population exhibits

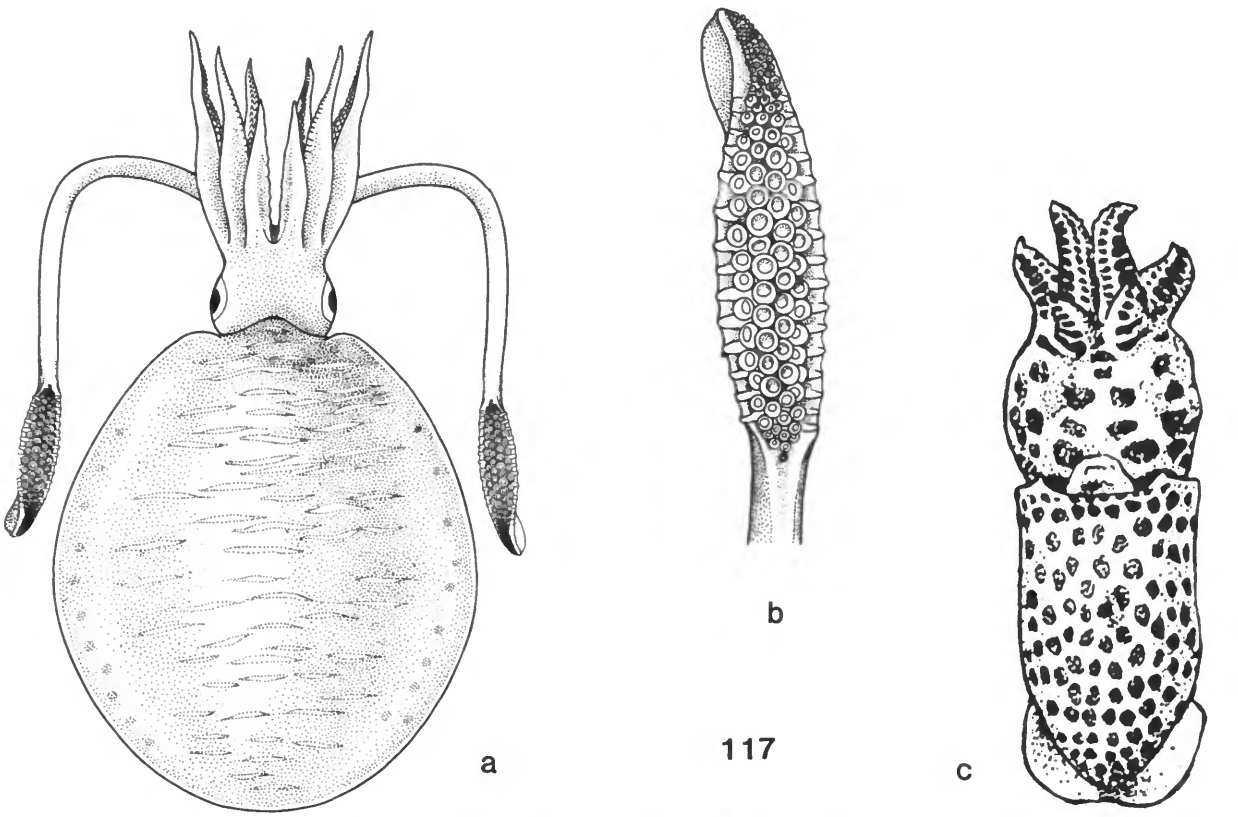


FIGURE 117.—*Sepioteuthis lessoniana: a*, dorsal view of adult; *b*, tentacular club of adult (both from Roper et al., 1984); *c*, ventral view of preserved hatchling, 10 mm ML (original drawing).

slight morphological differences, especially in terms of body proportions. This form is called *L. edulis* f. *budo* Wakiya and Ishikawa, 1921 (Figure 120). A synonym is *Loligo kensaki* Wakiya and Ishikawa, 1921.

Loligo chinensis Gray, 1849

SPECIES CHARACTERS.—*Adults* (Figure 121): Mantle elongate, robust; fin length about 70% ML with straight posterior margins; arm sucker rings with 10–15 sharp, conical teeth; largest tentacular suckers with 20–30 conical teeth; light organ on ink sac.

Young: No information available.

GEOGRAPHICAL DISTRIBUTION.—Western Pacific, southern Japan to northern and northeastern Australia.

REMARKS.—Synonyms are *L. etheridgei* Berry, 1918; *L. formosana* Sasaki, 1929.

Loligo bleekeri Keferstein, 1866

SPECIES CHARACTERS.—*Adults* (Figure 122): Mantle elongate; fin length about 60% ML with shallow, concave posterior margins; arm sucker rings with 10–14 quadrate teeth on distal margin; tentacles very weak with sucker rings carrying 20–30 blunt teeth; no light organ.

Young: Hatchling size is 3.3 mm ML (Okutani, pers. comm.); arm formula III, II, IV, I; color pattern distinct from hatchling of *L. japonica* in having larger number of yellow and red chromatophores.

GEOGRAPHICAL DISTRIBUTION.—All Japanese waters except northern Hokkaido; southern Korea.

Loligo japonica Hoyle, 1885

SPECIES CHARACTERS.—*Adults* (Figure 123): Mantle rather short and robust; fin length about 60% ML; arms II and III robust, especially in males, arm sucker rings with 9–11 semilunar teeth; tentacular club sucker rings with 18–23 blunt or semilunar teeth; no light organ.

Young: Hatchling size 2.0–2.6 mm ML; see *L. bleekeri* for chromatophore differences.

GEOGRAPHICAL DISTRIBUTION.—East China Sea, Taiwan to northern Japan, excluding northern Hokkaido.

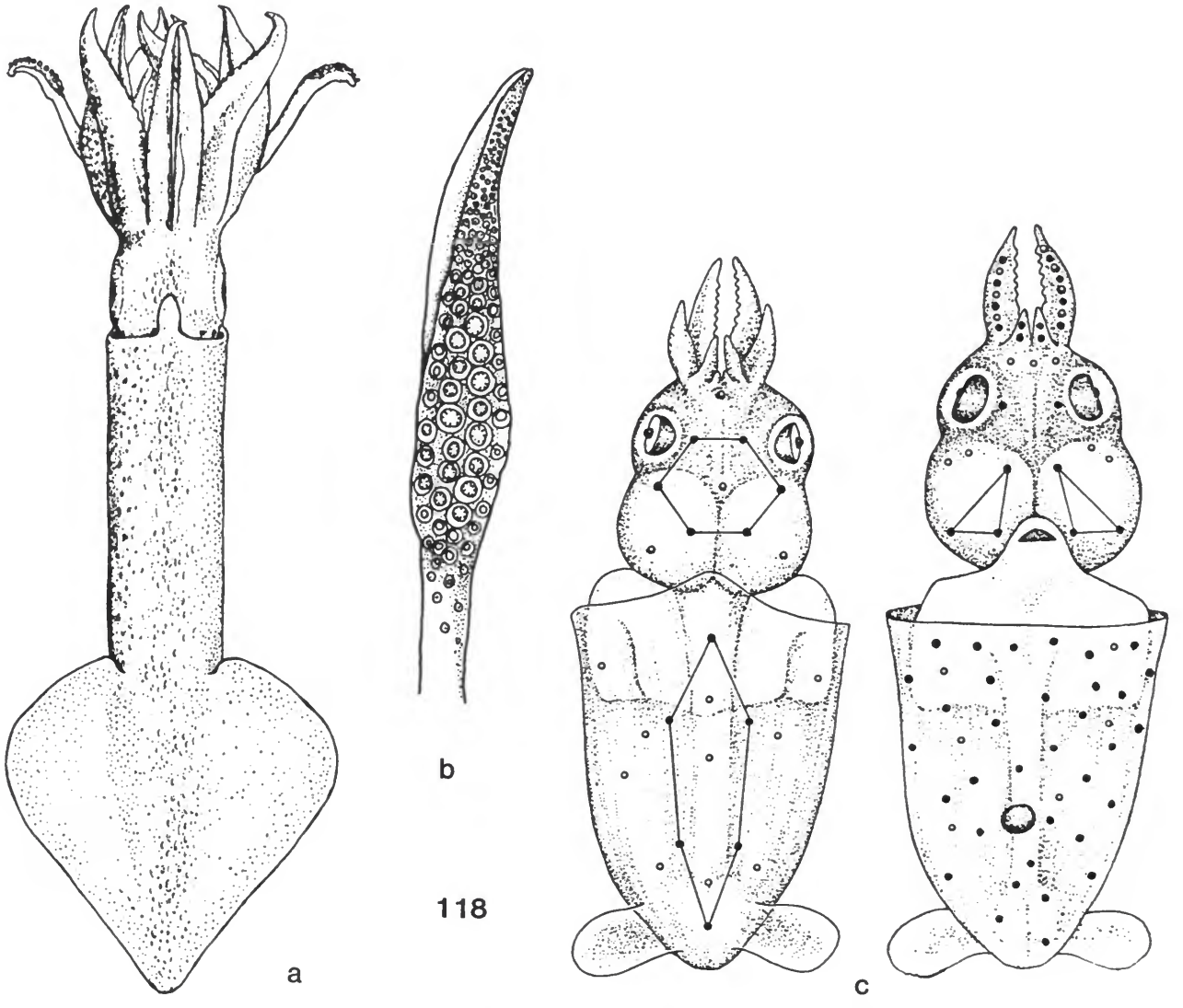


FIGURE 118.—*Loligo opalescens: a*, dorsal view of adult; *b*, tentacular club of adult (both from Roper et al., 1984); *c*, live hatchlings, 3.1 mm ML; closed circles = red chromatophores, open circles = yellow chromatophores, lines between chromatophores to show patterns (from McConathy et al., 1980).

Loligo sumatrensis Orbigny, 1835

SPECIES CHARACTERS.—*Adults* (Figure 124): Mantle rather short and robust (similar to *L. japonica*); arm suckers with 5–10 quadrate teeth of subequal height and width; tentacular suckers on central manus greatly enlarged and entirely smooth; no light organ.

Young: No information available.

GEOGRAPHICAL DISTRIBUTION.—Western Pacific.

REMARKS.—Synonyms are *L. kobiensis* Hoyle, 1885; *L. yokoyae* Ishikawa, 1926.

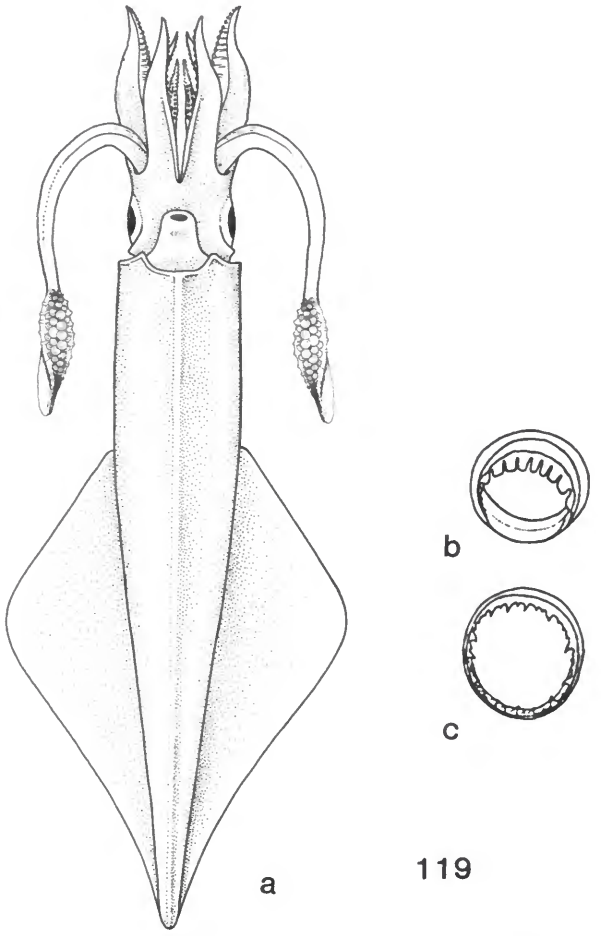
Loligo uyii Wakiya and Ishikawa, 1921

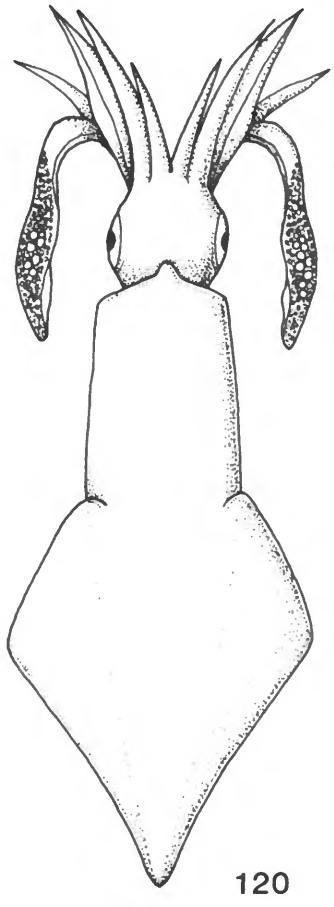
SPECIES CHARACTERS.—*Adults* (Figure 125): Very similar to *L. sumatrensis*; arm suckers with only 3–6 quadrate teeth, wider than high; rings of largest tentacular suckers lack teeth; no light organ.

Young: No information available.

GEOGRAPHICAL DISTRIBUTION.—Western Pacific, southern Japan, Yellow Sea to Hong Kong.

REMARKS.—Synonyms are *L. tagoi* Sasaki, 1929; *L. gotoi* Sasaki, 1929.





FIGURES 119, 120.—Western Pacific and Japanese loliginids: 119, *Loligo edulis: a*, ventral view of adult; *b*, arm sucker; *c*, tentacular sucker. 120, *L. edulis budo:* dorsal view of adult. (From Roper et al., 1984.)

Loligo beka Sasaki, 1929

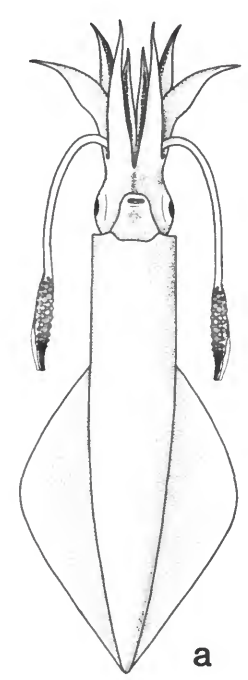
SPECIES CHARACTERS.—*Adults* (Figure 126): Small squid, similar to L. *sumatrensis;* arm suckers with only 3–5 quadrate to semilunar teeth, wider than high; the largest tentacular sucker rings with about 20 sharply pointed conical teeth; no light organ.

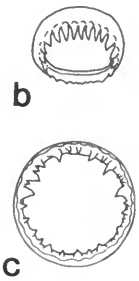
Young: No information available.

GEOGRAPHICAL DISTRIBUTION.—Southern Japan, Taiwan, Hong Kong.

REMARKS.—Natsukari (1983, 1984) created the genera *Nipponololigo* for *L. japonica, L. sumatrensis, L. uyii,* and *L. beka; Photololigo* for *L. edulis;* and *Heteroloiigo* for *L. bleekeri,* all largely based on the morphology of the hectocotylized arm and presence or absence of a light organ. Four species among eight are distributed further south to Southeast Asia, namely *L. edulis, L. chinensis, L. sumatrensis* and *Sepioteuthis lessoniana.* Brakoniecki (1986) revised the loliginid genera on the basis of hectocotylus morphology in conjunction with other characters. His conclusions differ substantially from those of Natsukari.

FIGURES 121–126 (opposite page).—Western Pacific and Japanese loliginids (cont.): *a*, ventral view; *b*, arm sucker; *c*, tentacular sucker. 121, *Loligo chinensis.* 122, *L. bleekeri.* 123, *L. japonica.* 124, *L. sumatrensis.* 125, *L. uyii.* 126, *L. beka.* (From Roper et al., 1984.)





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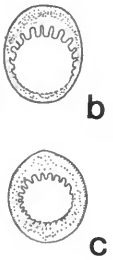

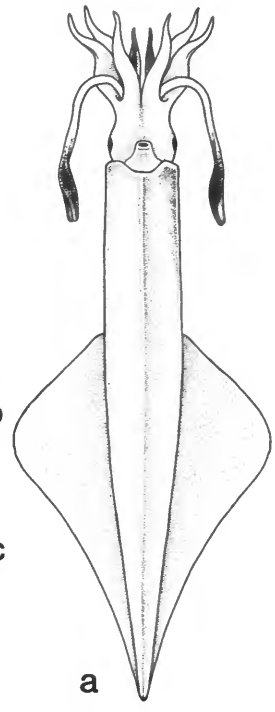

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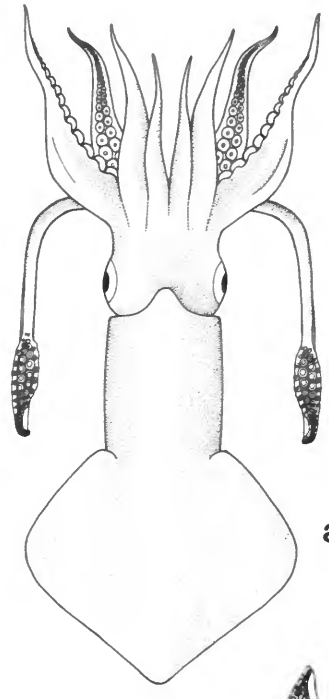

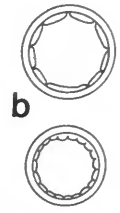

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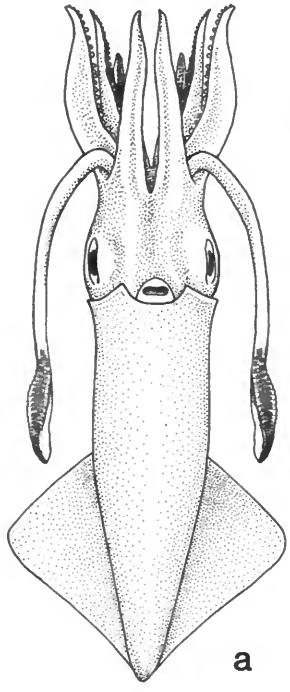

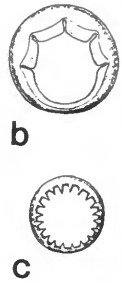

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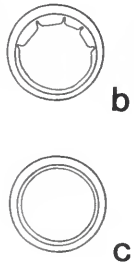

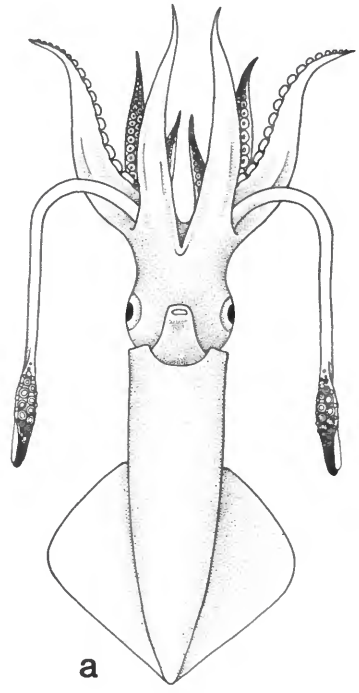

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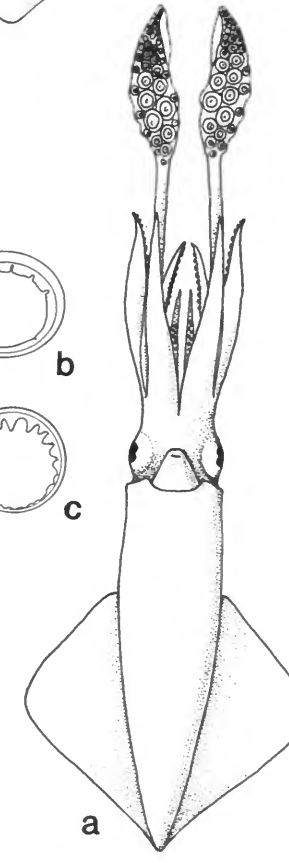

124

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Suborder OEGOPSIDA Orbigny, 1845

SUBORDINAL CHARACTERS.—Absence of a corneal membrane, thus the eyes are exposed directly to the sea; suckers generally absent on the buccal lappets (except in Bathyteuthidae and Ctenopterygidae); suckers with chitinous rings and/or hooks; female gonoducts paired; accessory nidamental glands absent (except in Ctenopterygidae).

The Enoploteuthid Group of Families

Family ENOPLOTHEUTHIDAE Pfeffer, 1900

Family ANCISTROCHEIRIDAE Pfeffer, 1912

Family PYROTEUTHIDAE Pfeffer, 1912

(by R.E. Young, K.M. Mangold, and M. Vecchione)

The taxa presented here as families have traditionally been considered to be subfamilies within the family Enoploteuthidae. Clarke (1988) proposed that the subfamilies be elevated to familial status. Distinctive differences in paralarval development among the proposed families support this proposal.

GROUP CHARACTERS.—*Adults:* Straight funnel locking-cartilages; arms with armature in 2 rows; hooks present on most arms; tentacular clubs with armature in 4 rows in juveniles (may be modified in adults); hooks present on clubs except in *Pterygioteuthis;* highly complex photophores; 8 buccal lappets; buccal connectives attach to dorsal borders of arms IV; adults mostly small.

Young: See characters of families.

GEOGRAPHICAL DISTRIBUTION.—Worldwide, tropical and temperate waters.

VERTICAL DISTRIBUTION.—Adults mesopelagic, undergo extensive vertical migrations; young inhabit upper 200 m.

Key to Families and Genera of the Enoploteuthid Group (Young)

1. Photophores on mantle, surface of head and arms (>4 mm ML), but not on viscera 2
   Photophores on viscera, but not on mantle, or surface of head or arms. PYROTEUTHIDAE 7
2. Photophores on mantle, head, eyes, and arms, but not on tentacles. ENOPLOTEUTHIDAE 3
   Photophores on mantle, head, arms, and tentacles, but not on eyes (>5–7 mm ML). ANCISTROCHEIRIDAE . . . . . ***Ancistrocheirus***
3. One or more enlarged photophores on distal tip of arms IV (>3–5 mm ML) 4
   No enlarged photophores on distal tip of arms IV . . . 6
4. Squid collected from seas around Japan 5
   Squid collected from other geographic regions . . . . . ***Abraliopsis***
5. Tentacle hooks in 2 rows (appear at about 5–10 mm ML) . . . . . ***Abraliopsis***
   Tentacle hooks in 1 row (appear at about 5 mm ML) . . . . . ***Watasenia***
6. Two enlarged photophores develop on eye (>2.5 mm ML) . . . . . ***Enoploteuthis***
   Three enlarged photophores develop on eye (>2.0–2.5 mm ML) . . . . . ***Abralia***
7. Photophores at base of gill present by at least 1.5 mm ML; gill photophores larger than anal photophores . . . . . ***Pterygioteuthis***
   Photophores at base of gill absent at <4–5 mm ML; gill photophores smaller than anal photophores . . . . . ***Pyroteuthis***

Family ENOPLOTEUTHIDAE Pfeffer, 1912

FAMILY CHARACTERS.—*Adults:* Nidamental glands absent; numerous small photophores over surfaces of mantle, funnel, head, and arms, but not on tentacles or viscera; conspicuous photophores present on ventral surface of eyeballs.

Young: Photophores develop in single row on each eye by 5 mm ML; numerous small photophores on ventral surface of mantle, funnel, head, and arms begin to appear at about 3–4 mm ML; photophores absent from tentacles and viscera.

Eggs: Members of the Enoploteuthidae are among the few squids that do not lay eggs in egg masses (Young and Harman, 1985). Individual eggs, surrounded by a layer of jelly, separately released into the plankton; eggs of different species vary slightly in size (0.9–1.5 mm maximum diameter) and shape (nearly circular to ellipsoidal in outline); eggs distinguished from fish and crustacean eggs by (1) lack of an oil globule, (2) near lack of a perivitelline space in early development, (3) nonspherical shape, (4) jelly layer or its remnant, and (5) homogeneous appearance of the yolk.

REMARKS.—Young *Abralia and Enoploteuthis* are not easily separated. The character used in the key (three versus two enlarged ocular photophores) works for the six species that we examined but may not hold for all species in these genera. Species of *Abraliopsis* that we examined can be separated from other genera not only by their enlarged photophores on the tips of the ventral arms, but also by their relatively longer arms (greater than or equal to mantle length) and tentacles. Characters in this family that are likely to be useful for separation of species include chromatophore patterns, size of largest club suckers relative to arm suckers, relative sizes among club suckers, number of club suckers, photophore patterns, and photophore sizes.

Enoploteuthis Orbigny, 1839

GENERIC CHARACTERS.—*Adults* (Figure 127*a*): Mantle with tail-like projection beyond posterior end of fin insertion; tentacular club hooks in 2 rows; suckers absent from manus of club; anterior and posterior ocular photophores enlarged, remaining ocular photophores small, subequal; enlarged photophores absent at tips of arms IV.

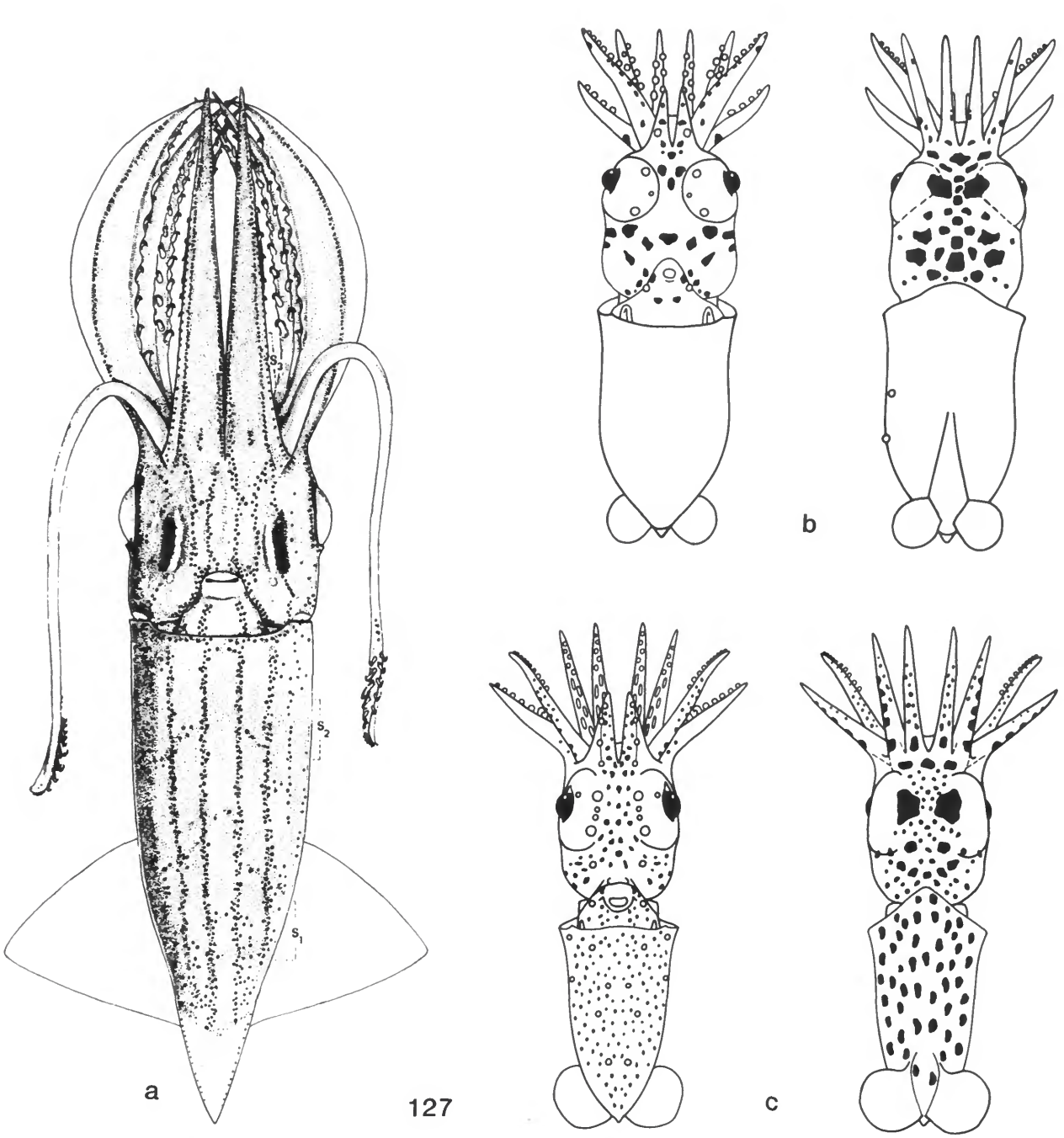


FIGURE 127.—Enoploteuthidae, *Enoploteuthis reticulata: a,* ventral view of adult female, 45.5 mm ML, 18°S, 126°W (from Okutani, 1974); *b,* ventral (left) and dorsal view, 2.8 mm ML, Hawaiian waters; *c,* ventral (left) and dorsal view, 4.1 mm ML, Hawaiian waters. (From Young and Harman, 1985.)

Young (Figures 127*b,c,* 128): Beyond about 10–15 mm ML, characteristic tail extends well beyond fins; tentacular hooks in 2 rows; approximately 9 ocular photophores; in Hawaiian species, development of ocular photophores begins with 2 photophores on each eye that develop into enlarged anterior and posterior ocular photophores.

Abralia Gray, 1849

GENERIC CHARACTERS.—*Adults* (Figure 129*a*): Fins extend to posterior end of mantle; manus of club with 1 row of hooks and 2 rows of suckers; ocular photophores of various sizes; enlarged photophores absent at tips of arms IV.

Young (Figures 129*b,* 130): By 10–15 mm ML, fins meet posteriorly; tentacular hooks in 1 row and ocular photophores variable in number and size; in Hawaiian species and at least some Atlantic species, development of ocular photophores begins with 3 photophores on each eye.

Abraliopsis Joubin, 1896

GENERIC CHARACTERS.—*Adults* (Figure 131*a,b*): Fins extend to posterior end of mantle; tentacular club hooks in 2 rows, with several small suckers between them; anterior and posterior ocular photophores enlarged, remaining ocular photophores small, subequal; ventral arms with 3 large photophores at tip.

Young (Figures 132, 133*a–d*): Large photophores present on tips of arms IV by 3–5 mm ML; relatively long arms and tentacles.

Watasenia Ishikawa, 1913

GENERIC CHARACTERS.—*Adults* (Figure 134*a*): Fins extend to posterior end of mantle; tentacular club with only 2 hooks in 1 row, remaining armature of club comprised of suckers; anterior and posterior ocular photophores enlarged, remaining ocular photophores small, subequal; 3 large photophores at tip of arms IV.

Young (Figure 134*b–c*): General appearance similar to that of *Abraliopsis* species. Photophores develop at tip of arms IV by 5 mm ML; tentacular hooks appear at 4.5 mm ML.

REMARKS.—A single species only known from the waters surrounding Japan.

Family ANCISTROCHEIRIDAE Pfeffer, 1912

FAMILY CHARACTERS.—*Adults:* Nidamental glands present; large photophores scattered on ventral surface of mantle, funnel, head, and tentacles, but not eyes; numerous minute photophores also scattered on surface of mantle, head, and arms IV; photophores absent from eyeballs and viscera; head and mantle with gelatinous tissues; posterior end of mantle elongate, forms tail; fins very large.

Young (Figure 135): Tentacular suckers few but large; eyes separated from arm bases, with space between filled by gelatinous head tissue; digestive gland kidney bean-shape, located in posterior of mantle cavity; head and mantle photophores present by 5–6 mm ML in both Hawaiian and Atlantic paralarvae; diagnostic tentacular photophores appear by 7 mm ML; arm and tentacular hooks present by 9 mm ML.

Ancistrocheirus Gray, 1849

GENERIC CHARACTERS.—See family characters.

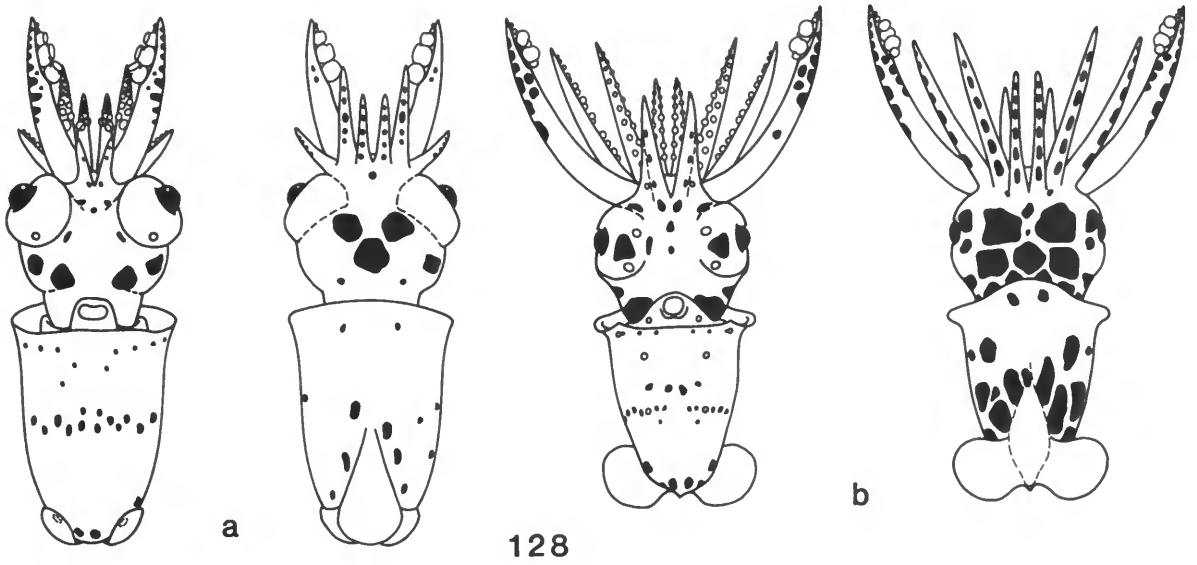
REMARKS.—A single species, *Ancistrocheirus lesueuri* (Orbigny, 1848) generally is recognized in this family (see, however, Nesis, 1982). The young of this species were described as *Thelidioteuthis alessandrini* (Verany, 1851). Differences in paralarvae from different oceans (Figure 135) suggest that more than one species of *Ancistrocheirus* exists. These paralarvae bear little resemblance to those of the other families treated in this chapter. The relatively small, broadly spaced eyes, the separation of the eyes from the arm bases, the gelatinous head tissues, and the posterior position and kidney bean-shape digestive gland are distinctive within the group of families. Very young specimens can be easily confused with young of the Octopoteuthidae due to the similarities of the head, club structure, and fin size. Like *Ancistrocheirus,* paralarval octopoteuthids are characterized by gelatinous head tissue and tentacular clubs with relatively few suckers, which are large compared with those of other paralarvae, although the club suckers of octopoteuthids are fewer and larger than those of *Ancistrocheirus.* However, the peculiar disc-shape digestive gland of octopoteuthids and the tentacular photophores of *Ancistrocheirus* allow their separation.

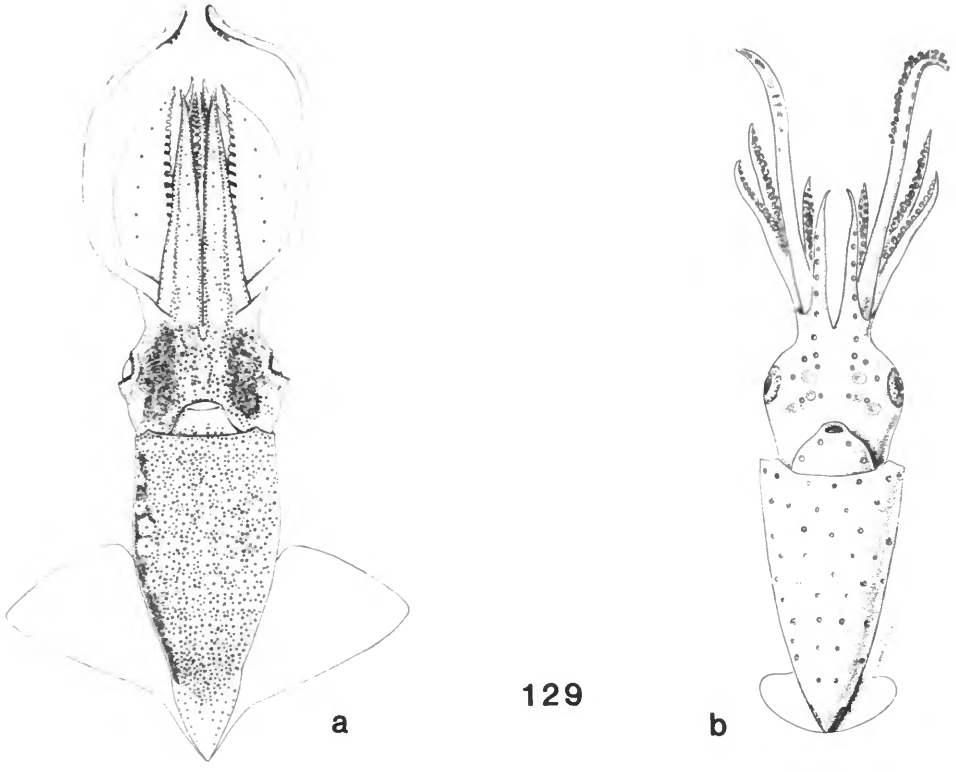
Family PYROTEUTHIDAE Pfeffer, 1912

FAMILY CHARACTERS.—*Adults:* Nidamental glands present; only one oviduct developed; photophore present on viscera; conspicuous photophores arranged in complex patterns on ventral surface of eyeballs; photophores embedded in tentacular stalk but absent from surface of mantle, funnel, head, and arms; posterior end of mantle extends into acute tail supported by needle-like terminal conus of gladius; fins rounded.

Young: Photophores on eyes (present by 1–2 mm ML) develop into complex pattern; conspicuous photophores present on viscera at 2–3 mm ML; photophores absent from mantle and arms; photophores deeply embedded in tentacle but appear only late in development; ocular and anal photophores often highly iridescent (see color figures in Chun, 1910).

REMARKS.—The young have very small tentacular clubs that generally curl dorsally at the tip and are covered with very small suckers. The tentacular stalk usually has a ventrally directed bend or "elbow" in the proximal half. These features often allow identification to family even in badly damaged





FIGURES 128, 129.—Enoploteuthidae: 128, *Enoploteuthis higginsi: a*, ventral (left) and dorsal view, 2.2 mm ML, Hawaiian waters; *b*, ventral (left) and dorsal view, 3.5 mm ML, Hawaiian waters (both from Young and Harman, 1985). 129, *Abralia* spp.: *a*, *Abralia andamanica* ventral view of adult male, 31.1 mm ML, 5°N, 98°W (from Okutani, 1974); *b*, *Abralia* sp. ventral view, 4.5 mm ML, NW Atlantic (unpublished).

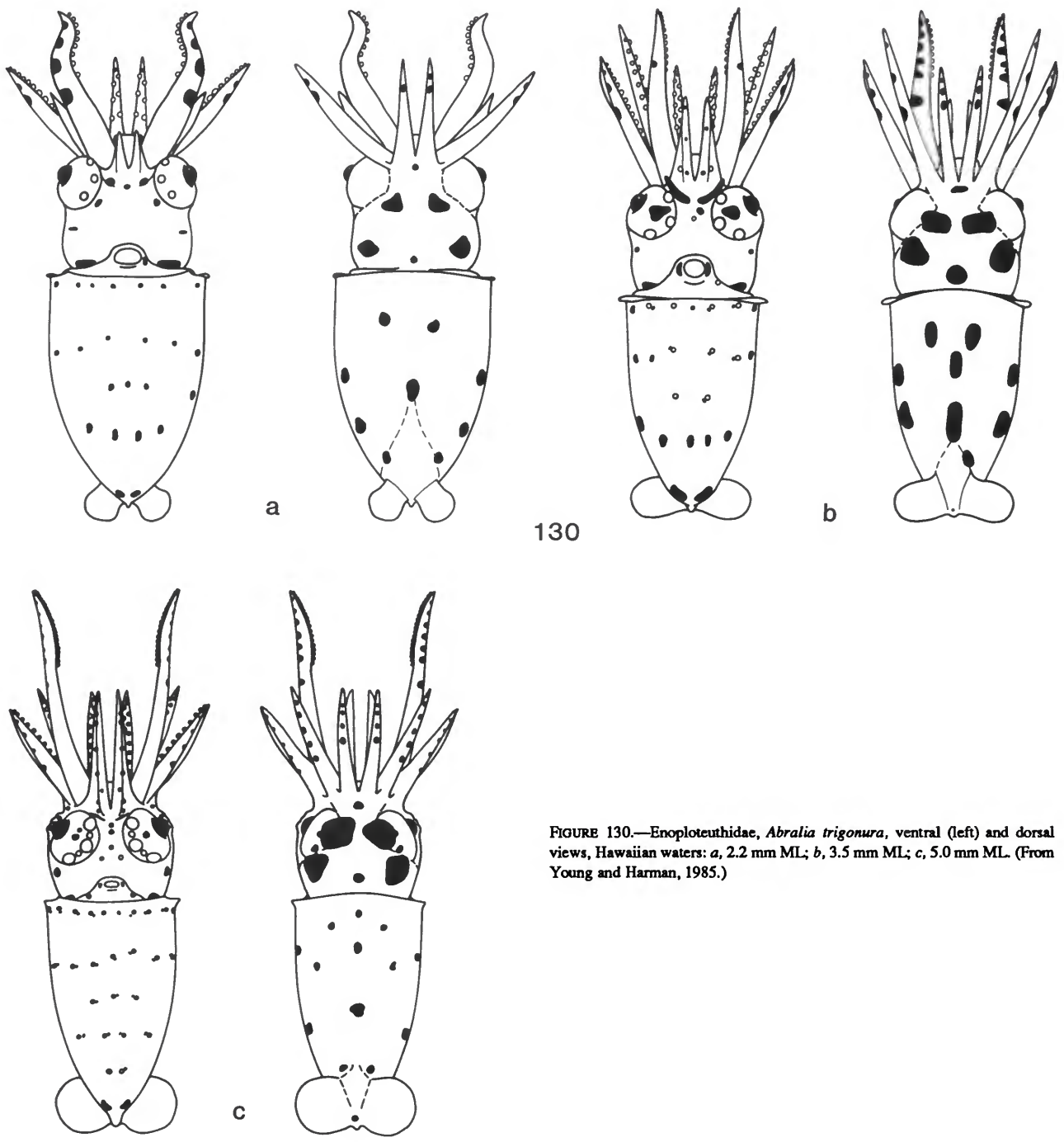
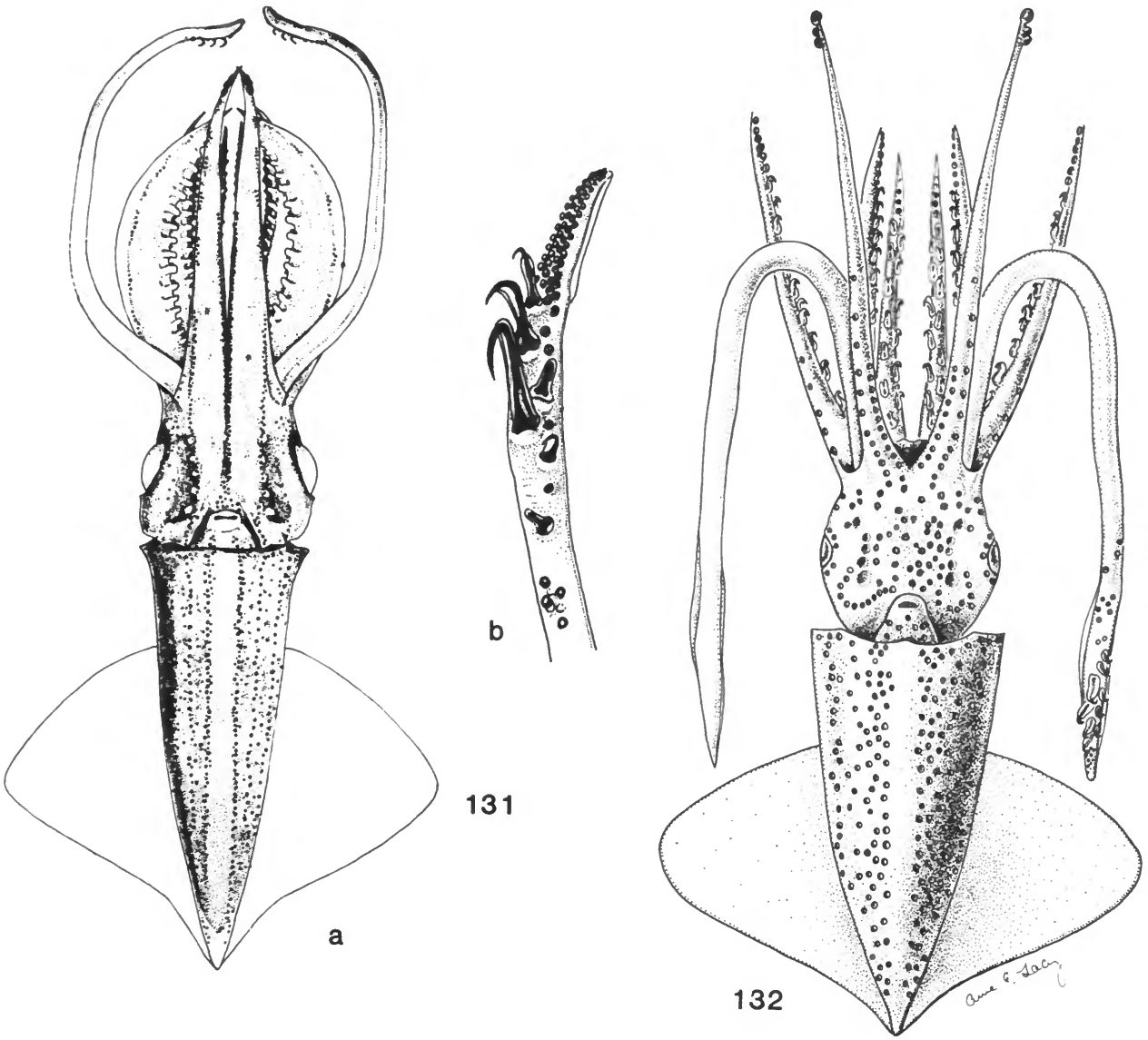


FIGURE 130.—Enoploteuthidae, *Abralia trigonura*, ventral (left) and dorsal views, Hawaiian waters: *a*, 2.2 mm ML; *b*, 3.5 mm ML; *c*, 5.0 mm ML. (From Young and Harman, 1985.)



FIGURES 131,132.—Enoploteuthidae, *Abraliopsis* spp.: 131, *A. falco: a,* ventral view of adult female, 40.0 mm ML, 17°N, 126°W; *b,* tentacular club of male, 29.0 mm ML, 11°N, 112°W (both from Okutani, 1974). 132, *A. pfefferi:* ventral view, 13 mm ML, NW Atlantic (unpublished).

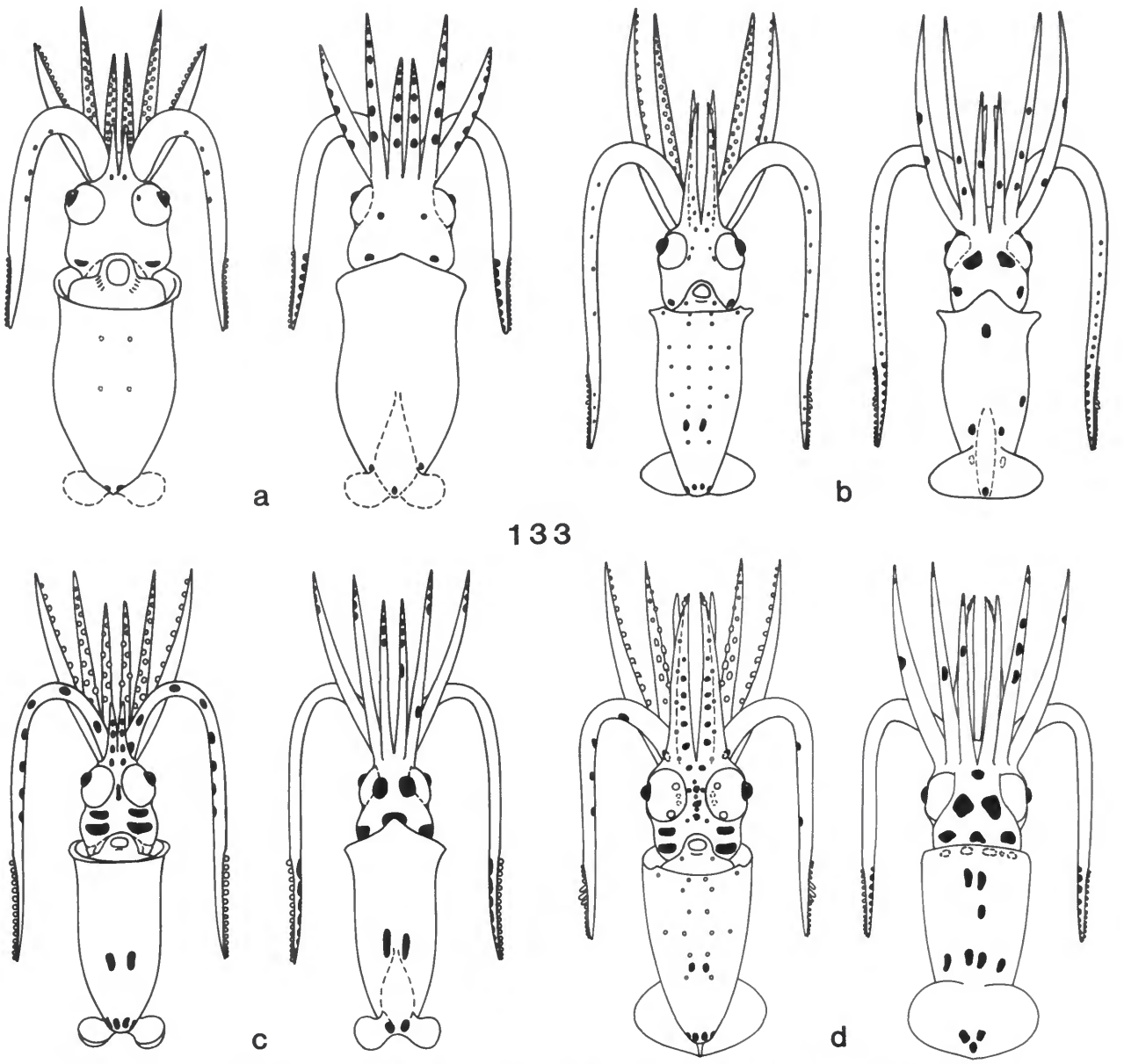


FIGURE 133.—Enoploteuthidae, *Abraliopsis* spp., ventral (left) and dorsal views, Hawaiian waters: *a,b*, *Abraliopsis* sp. A.: *a*, 3.0 mm ML; *b*, 4.6 mm ML. *c,d*, *Abraliopsis* sp. B.: *c*, 3.0 mm ML; *d*, 4.6 mm ML. (From Young and Harman, 1985.)

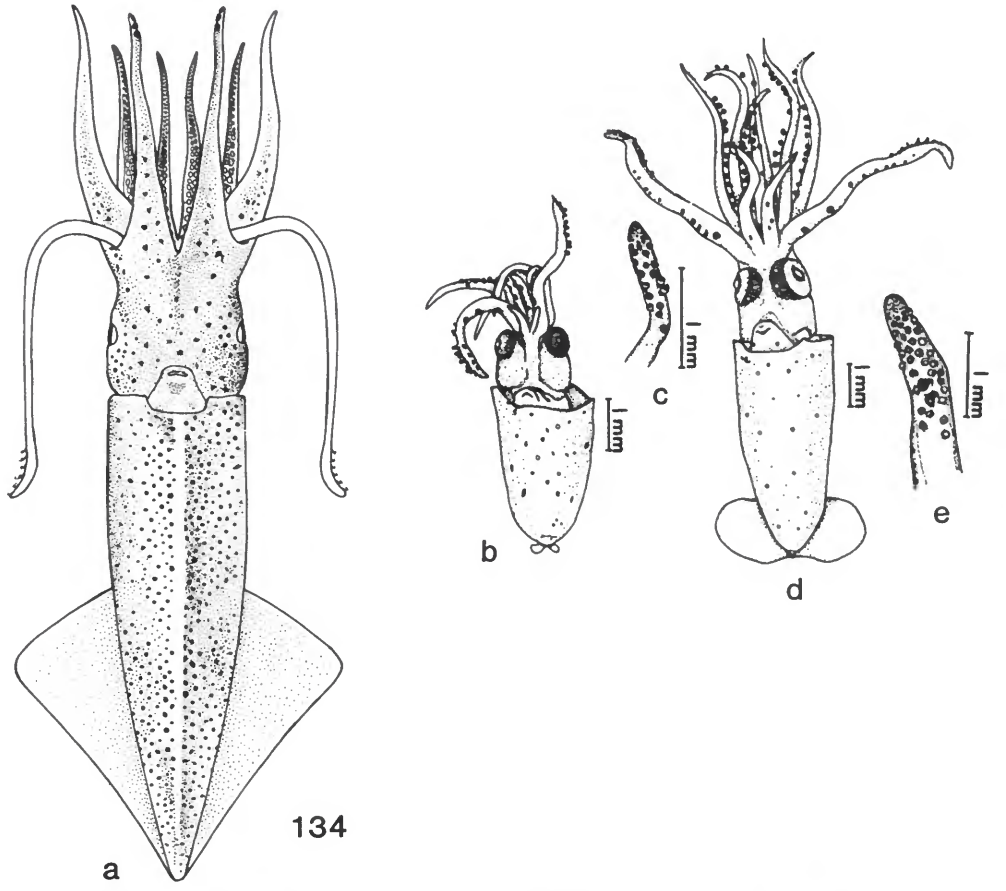
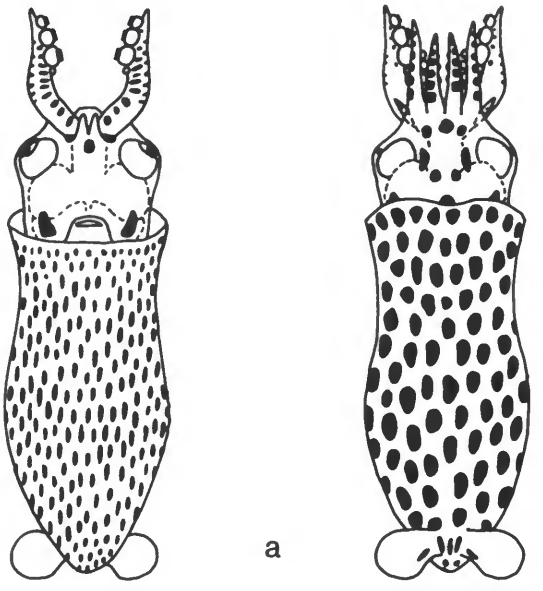


FIGURE 134.—Enoploteuthidae, *Watasenia scintillans: a*, ventral view of adult (from Roper et al., 1984); *b*, ventral view, 3.3 mm ML; *c*, tentacular club of same; *d*, ventral view, 5.5 mm ML; *e*, tentacular club of same (*b–e*, from Kubodera and Okutani, 1981).

FIGURE 135 (opposite page).—Enoploteuthidae, *Ancistrocheirus* sp.: *a*, ventral (left) and dorsal views, 2.8 mm ML, Hawaiian waters; *b*, ventral view and tentacular club, 5.0 mm ML, NW Atlantic; *c*, ventral (left) and dorsal view, 6.2 mm ML, Hawaiian waters (*a–c*, unpublished); *d*, ventral view, 29.0 mm ML, E. Pacific (from Okutani, 1974).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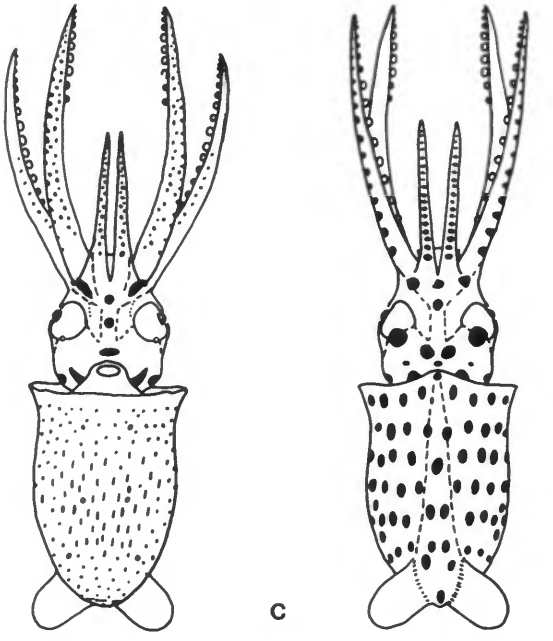
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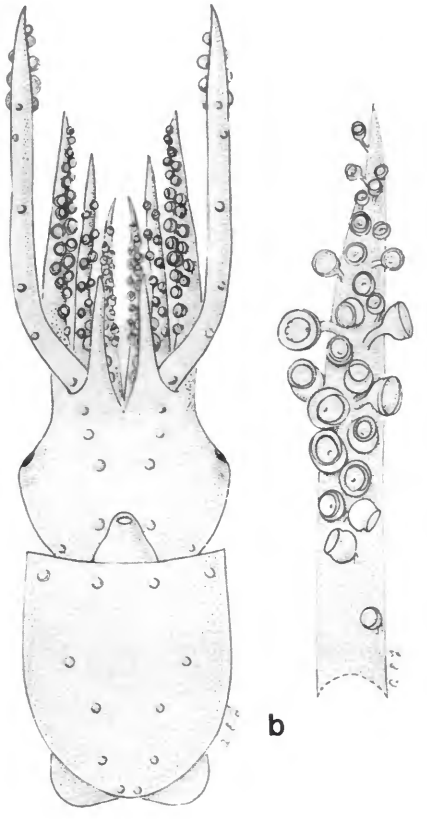
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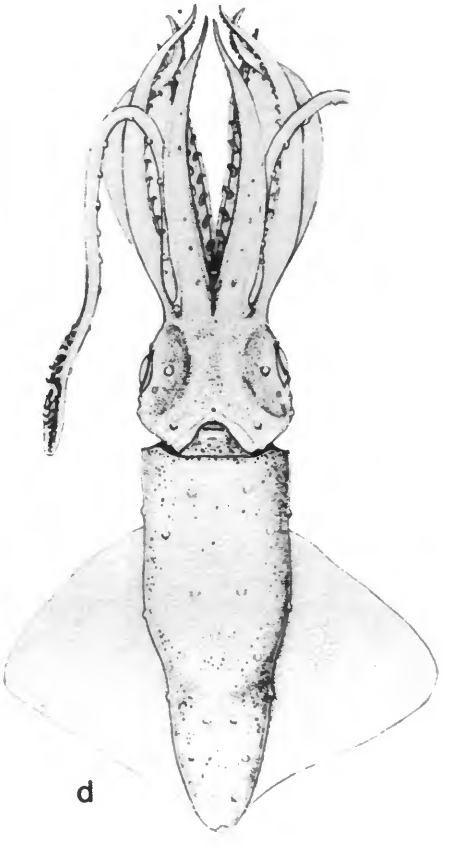
d

specimens. The arm suckers also are very small. By 4–6 mm ML the posterior tip of the mantle is sharply pointed, and the fins have the distinctive appearance (i.e., free posterior lobes) of the adult.

Specimens of these genera can be difficult to separate in the youngest stages. We find that chromatophore patterns are very helpful but these may be of specific rather than generic value. The most useful method of separating genera is by the presence, and in larger specimens, the size of gill photophores (Figure 137*b*). Unfortunately, the mantle must be cut open to examine these organs and some experience is needed to recognize these photophores in the smallest specimens. Other characters of specific value include size of the ocular photophores, mantle length at which the ocular photophores first appear, and relative size among club suckers.

Although only six species presently are recognized in this family, their paralarvae are abundant. In tropical oceanic waters, these paralarvae may be among the numerically dominant cephalopods in the plankton.

Pyroteuthis Hoyle, 1904

GENERIC CHARACTERS.—*Adults* (Figure 136*a*): Hooks present in 1 row on tentacular clubs; hooks on arms in 2 rows over almost entire length, including arms IV; 12 photophores on ventral surface of eyeballs; only left oviduct developed; right arm IV hectocotylized.

Young (Figure 136*b*): Gill photophores absent at <4–5 mm ML; gill photophores smaller than anal photophores in larger specimens; medial ocular photophores absent at <5 mm ML; minimum separation of fins about 0.3–0.5 mm at 2–6 mm ML.

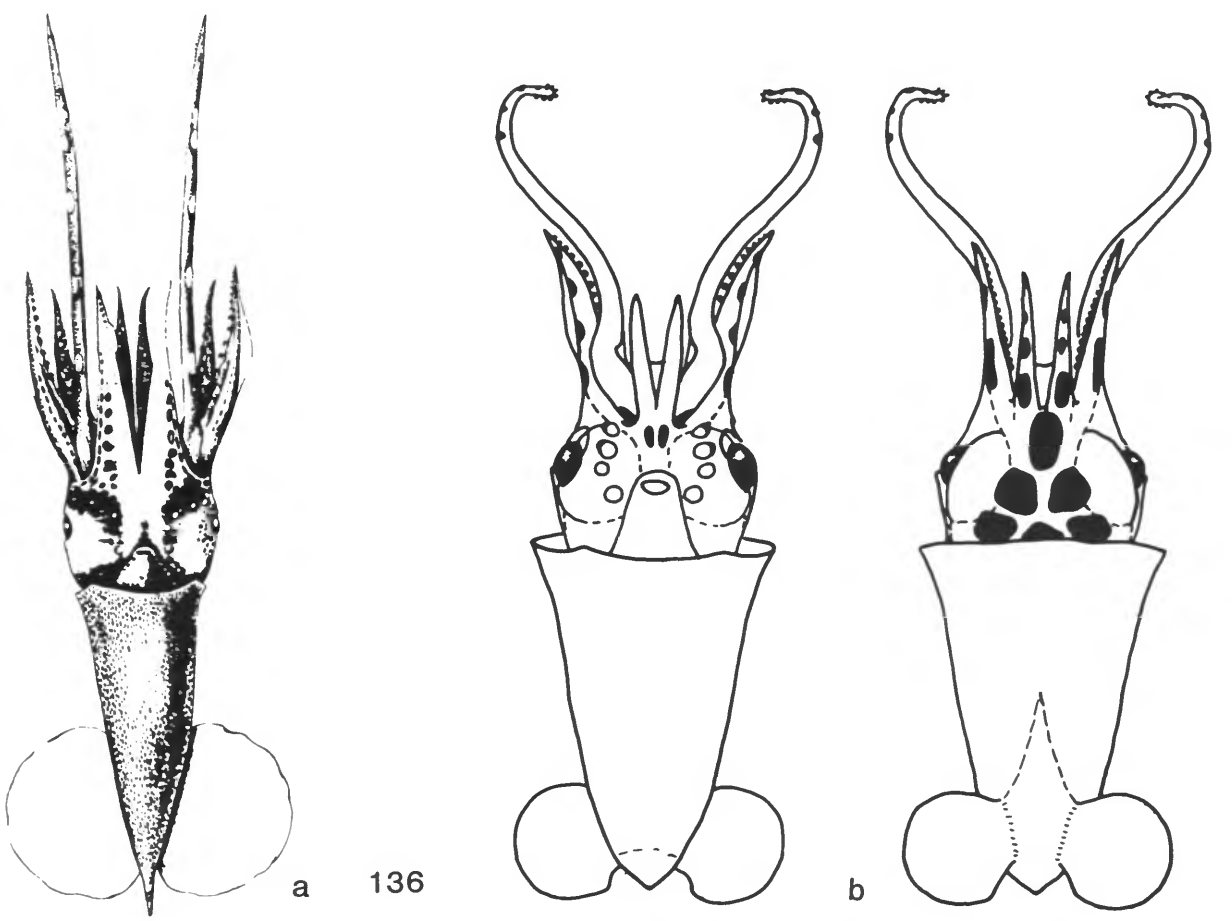

FIGURE 136.—Enoploteuthidae, *Pyroteuthis addolux: a*, ventral view of adult, 30 mm ML, holotype (from Young, 1972); *b*, ventral (left) and dorsal views, 2.9 mm ML, Hawaiian waters (unpublished).

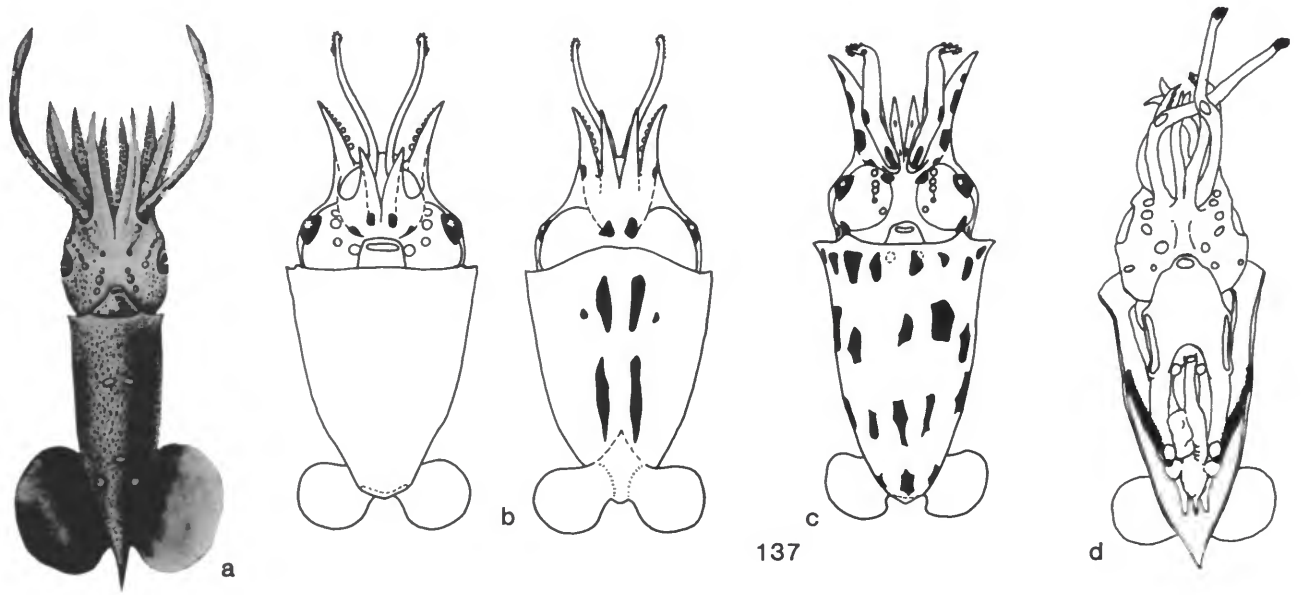

FIGURE 137.—Enoploteuthidae, *Pterygioteuthis* spp.: *a*, *P. gemmata*, ventral view of adult, 23 mm ML, E. Pacific (from Young, 1972); *b*, *P. giardi*, ventral (left) and dorsal views, 2.9 mm ML, Hawaiian waters (unpublished); *c*, *P. microlampas*, ventral view, 2.9 mm ML, Hawaiian waters (unpublished); *d*, *Pterygioteuthis* sp., ventral view with mantle removed to show anal light organs and gill light organs, 5 mm ML, NW Atlantic (unpublished).

Pterygioteuthis Fischer, 1896

GENERIC CHARACTERS.—*Adults* (Figure 137*a*): Tentacular clubs without hooks; arm hooks few, only in middle of arms I-III, no more than 2 hooks on arm IV; 14–15 photophores on ventral surface of eyeballs; only right oviduct developed; left arm IV hectocotylized.

Young (Figure 137*b–d*): Gill photophores present at 1.5 mm ML; gill photophores as large as or larger than anal photophores; medial ocular photophores absent at <2–3 mm ML; minimum separation of fins 0.1–0.2 mm at 2–6 mm ML.

REMARKS.—The distinctive difference in the separation of the fins can only be relied upon in nearly perfect specimens; slight damage to the fin attachment in *Pterygioteuthis* can cause it to mimic the *Pyroteuthis* condition. In freshly caught specimens a pink patch occurs at the base of each tentacle and on the carpus in *Pyroteuthis*. Pink patches do not occur in *Pterygioteuthis*.

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Family LYCOTEUTHIDAE Pfeffer, 1908

(by G.L. Voss and S.J. Stephen)

FAMILY CHARACTERS.—*Adults:* Simple funnel locking-apparatus; biserial arm suckers; tetraserial club suckers; photophores on viscera, ventral surface of eyes, and on mantle, arms, and tentacles of some species.

Young: No distinct "larval" stage, but usually recognizable at or before 3.0–3.5 mm ML by large central photophore on ventral eyeball (except in *Lampadioteuthis;* see Young, 1964); central photophore develops earliest, is larger and different from others in color and surface sculpture.

Eggs: Unknown.

Key to Subfamilies, Genera, and Species of LYCOTEUTHIDAE (Adults)

(Emended from Voss, 1962)

1. Four photophores on eyeball, 3 in line on ventral periphery, 1 lateral. Lampadioteuthinae [Figure 138*a*] . . . . . ***Lampadioteuthis megaleia***
   Five photophores in single line on ventral periphery of eyeball. LYCOTEUTHINAE 2
2. Terminal posterior photophore between fins; single photophore on tips of arms II and III in males; arms subequal in both sexes [Figure 139] . . . . . ***Selenoteuthis scintillans***
   No terminal posterior photophore between fins; no terminal photophore on arm tips of males 3
3. Arms III greatly elongate in both males and females [Figure 138*g*] . . . . . ***Nematolampas regalis***
   Arms subequal in females (unknown in *Lycoteuthis lorigera*), without integumentary photophores; males with arms II greatly elongate, posterior end of mantle elongated into slender tail; integumentary photophores present [Figure 138*b–f*] . . . . . ***Lycoteuthis diadema***
   Females unknown; males with integumentary photophores on elongate second arms, integument missing over rest of body, no elongate slender tail . . . . . ***Lycoteuthis lorigera***

Subfamily LAMPADIOTEUTHINAE Berry, 1916

Lampadioteuthis megaleia Berry, 1916

SPECIES CHARACTERS.—*Young:* Juvenile specimens recorded with mantle lengths of 4.5–13 mm ML. At 8.0 mm ML (Figure 138*a*) eye with 3 photophores in line, the anterior one slightly larger, a single lateral photophore between and posterior to other photophores and eye lens; fins broadly oval in outline.

GEOGRAPHICAL DISTRIBUTION.—Western South Pacific, Kermadec Islands (stranded on beach); eastern North Atlantic from areas 25°N–33°N, 20°W–32°W, between Spain and Azores; western North Atlantic from 39°N–41°N, 56°W–63°W.

VERTICAL DISTRIBUTION.—No diel migration known, apparently upper mesopelagic and epipelagic (eastern Atlantic).

REFERENCES.—Voss (1962), Young (1964), Stephen (1982), Herring et al. (1985).

Subfamily LYCOTEUTHINAE Pfeffer, 1908

Key to Species of LYCOTEUTHINAE ("Larvae" and Early Juveniles, excluding *Lycoteuthis lorigera* and *Nematolampas)*

At 4.0 mm ML: 5 photophores on ventral periphery of eye; no visceral photophores visible; fins separate, small, laterally pointed. At 5.5 mm ML: 4 visceral photophores present; posterior margins of fins nearly straight transversely. At 8 mm ML: fin margins straight posteriorly, convex anteriorly. No terminal mantle photophore [Figure 138*b–f*] . . . . . ***Lycoteuthis diadema***

At 3.5 mm ML: 3 photophores on ventral periphery of eye, median one markedly larger than others; 4 visceral photophores; fins separate, paddle-shape; minute, clear, incipient terminal photophore at posterior end of mantle. At 6.0 mm ML: 5 photophores on each eye; fins transversely elliptical, narrow, laterally pointed; distinct dark photophore on posterior tip of mantle [Figure 139] . . . . . ***Selenoteuthis scintillans***

Lycoteuthis diadema (Chun, 1900)

SPECIES CHARACTERS.—*Young* (Figure 138*b–f*): Earliest identifiable specimens (4 mm ML) (Figure 138*b*) have all 5 photophores on eyeball, of which median one is largest and differs from others in surface texture and opalescent color; no visible photophores on viscera within mantle; mantle somewhat narrow, elongate; fins small, lateral, apical; eyes large and protruding. At 5.5 mm ML (Figure 138*c,d*) central ocular photophore noticeably larger than others, with opalescent, pinkish color; 4 photophores visible on viscera, 1 each side of rectum and 2 abdominal; mantle stout; fins larger. At 8.0 mm ML (Figure 138*e, f*) 4 abdominal photophores, median two large, lateral two small; fins nearly straight along posterior margins, convex anteriorly.

GEOGRAPHICAL DISTRIBUTION.—Worldwide between about 40°N and 46°S.

VERTICAL DISTRIBUTION.—Most specimens have been taken in open nets with estimated depths of 300–600 m. Captures of "larvae" have been in the upper 200 m.

REFERENCES.—Voss (1962), Roper and Young (1975), Toll (1983).

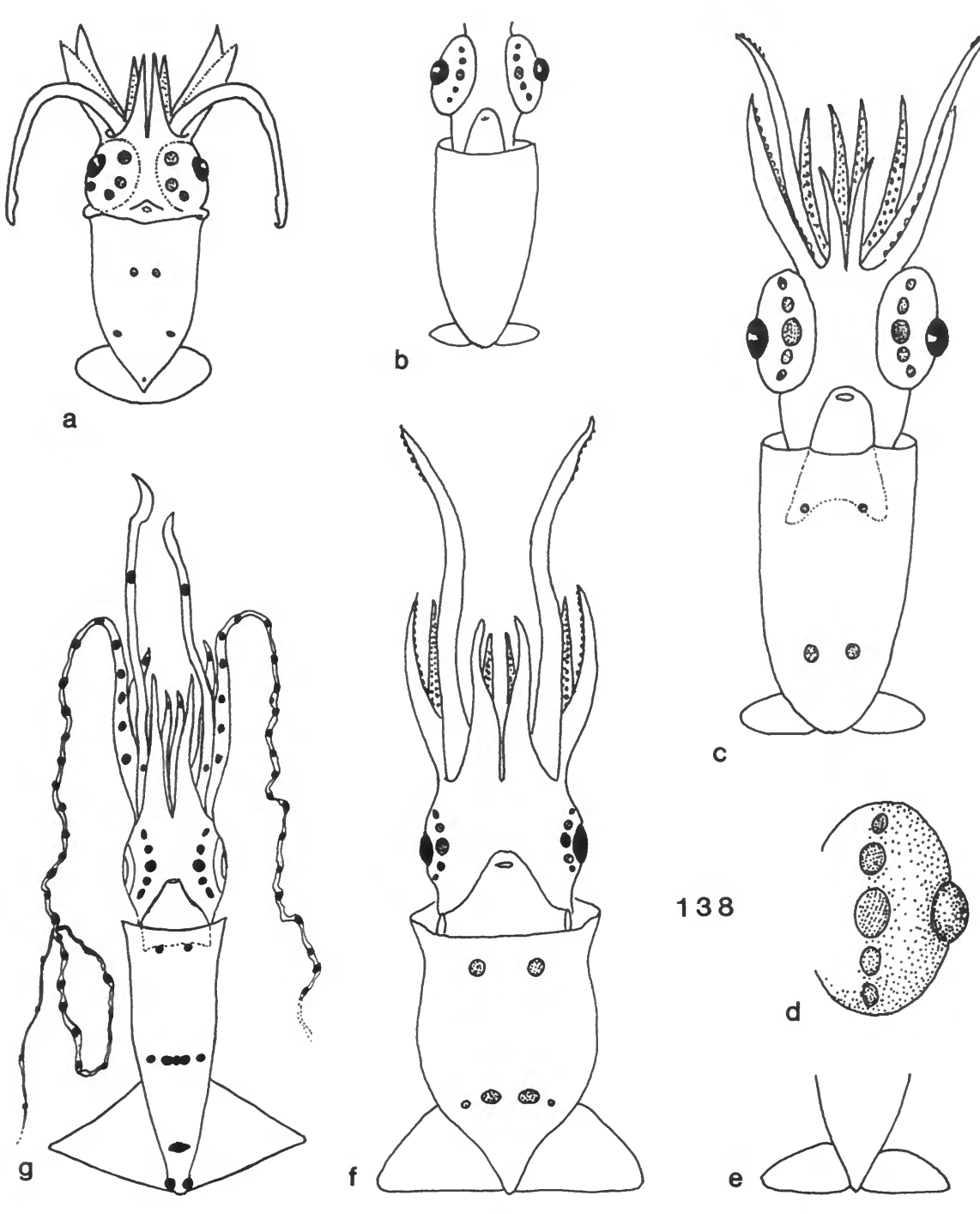

FIGURE 138.— Lycoteuthidae: *a, Lampadioteuthis megaleia,* ventral view, 8.0 mm ML (redrawn from Young, 1964). *b–f, Lycoteuthis diadema: b,* ventral view, 4.0 mm ML, 27°N, 54°W; *c,* ventral view, 5.5 mm ML, 16°N, 61°W; *d,* left eye of same; *e,* fins, 8.0 mm ML specimen; *f,* ventral view, 8.0 mm ML (*b–f,* redrawn from Voss, 1962). *g, Nematolampas regalis:* ventral view, 32 mm ML, holotype, Kermadec Islands (from Berry, 1913).

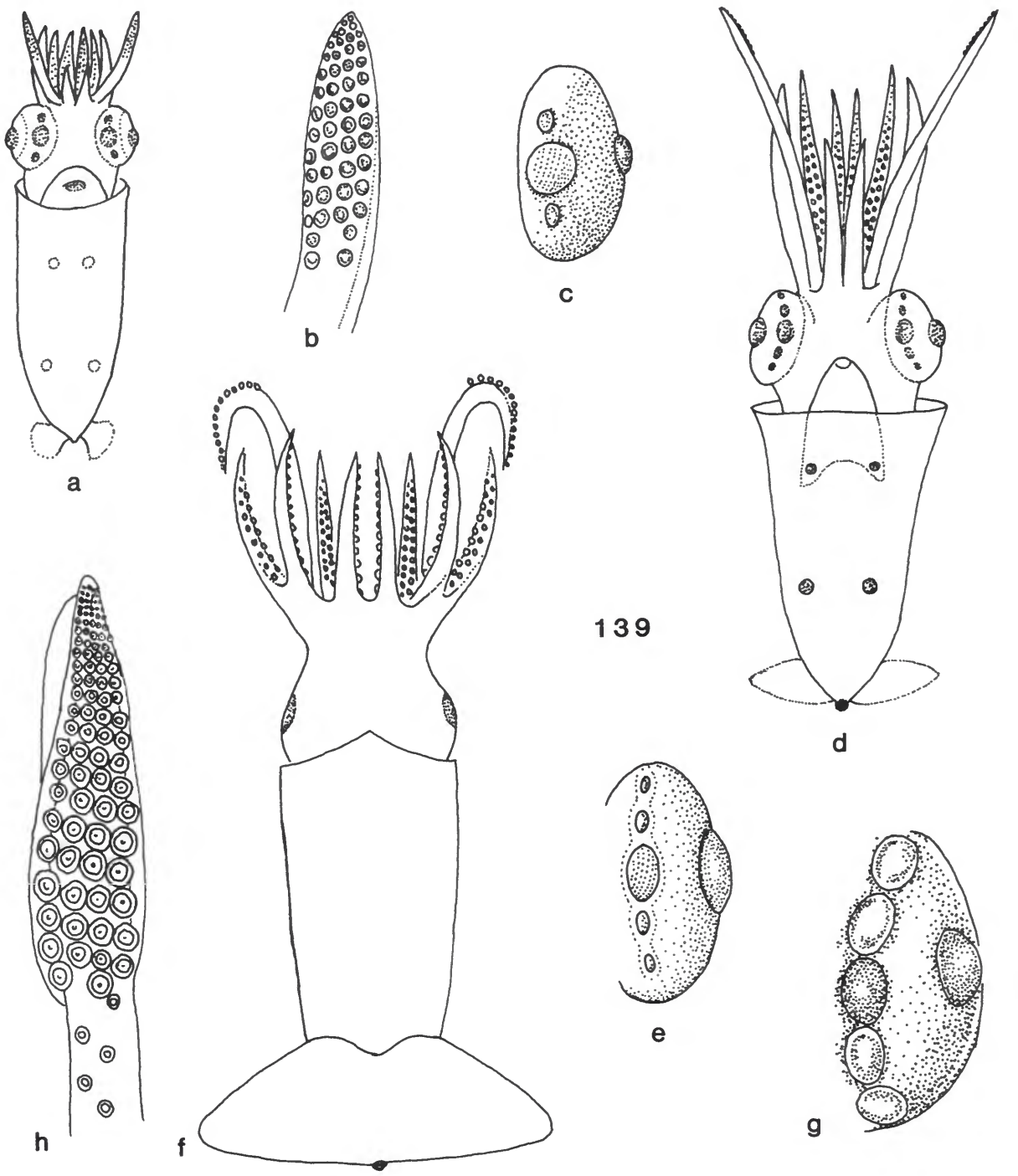

FIGURE 139.—Lycoteuthidae, *Selenoteuthis scintillans* (*a–c*, 3.5 mm ML, 17°N, 64°W; *d,e*, 6.0 mm ML, same station; *f–h*, 9.3 mm ML, USNM 730510): *a*, ventral view; *b*, tentacluar club; *c*, left eye; *d*, ventral view; *e*, left eye; *f*, ventral view; *g*, left eye; *h*, tentacular club (redrawn from G. Voss, 1958).

Lycoteuthis lorigera (Steenstrup, 1875)

SPECIES CHARACTERS.—*Adults:* Species known only from single male taken in the "South Sea" (= Pacific Ocean) from a whale stomach.

Young: Unknown.

REMARKS.—Beaks referred to this species by Imber (1975) have not been verified.

REFERENCES.—Voss (1962), Imber (1975), Toll (1983).

Selenoteuthis scintillans Voss, 1958

SPECIES CHARACTERS.—*Young* (Figure 139): Specimens from Nesis (1975) of 1.2–1.5 mm ML with single photophore on eye probably are this species. Earliest positively identifiable specimens (3.5 mm ML) (Figure 139*a–c*) with 3 photophores on eyeball of which median one markedly larger than other two, its surface faceted and opalescent; pair of photophores on anterior end of digestive gland hidden by base of funnel; 3 photophores on abdomen; a small, clear, incipient terminal photophore on mantle tip between fins; fins paddle-shape; mantle elongate; tentacular clubs not expanded. At 6.0 mm ML (Figure 139*d,e*) all 5 ocular photophores present; visceral photophores as in 3.5 mm specimen, better developed; terminal photophore distinct, darkly pigmented; fins lateral with both margins convex, pointed laterally. At 9.0 mm ML (Figure 139*f–h*) all visceral photophores present; clubs expanded; fins broadly transverse, elliptical, pointed laterally.

GEOGRAPHICAL DISTRIBUTION.—Widely distributed in the western North Atlantic from about 8°N through Caribbean Sea to south of Gulf Stream and in warm-core eddies northward to eastern Canada 39°N–41°N, 55°W–65°W; fewer in eastern North Atlantic from about 30°N–33°N and 31°W–63°W.

VERTICAL DISTRIBUTION.—Juveniles and adults perform diel migrations; occur at night in depths shallower than 200 m but descend to 300–700 m during day; larger specimens may occur somewhat deeper than smaller ones.

REFERENCES.—Voss (1958, 1962), Cairns (1976), Clarke and Lu (1975), Roper and Young (1975), Nesis (1975), Lea (1978, 1984), Lu and Roper (1979), Herring et al. (1985), Stephen (1982).

Nematolampas regalis Berry, 1913

SPECIES CHARACTERS.—*Adults* (Figure 138*g*): Species known only from stranded specimens in Kermadec Islands.

Young: Not known.

GEOGRAPHICAL DISTRIBUTION.—Western South Pacific at Sunday Island, Kermadec Islands 25°26′S, 175°09′W.

VERTICAL DISTRIBUTION.—Stranded on beach and from 48 m (Herring et al., 1985). Apparently mesopelagic.

REMARKS.—Originally described from Kermadec Islands, no new material reported until 1985 when Herring et al. received two specimens (22 and 23 mm ML) from Imber and Lu. Herring et al. stated that there were no discernible differences in the photophores between the sexes.

REFERENCES.—Berry (1913, 1914), Voss (1962), Herring et al. (1985).

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Family HISTIOTEUTHIDAE Verrill, 1881

(by N.A. Voss, S.J. Stephen, and Zh. Dong)

FAMILY CHARACTERS.—Mantle usually thick-walled, short, and conical; head large, with large eyes asymmetrically developed, left larger than right in large juvenile to adult animals; fins terminal, medium to large, together transversely oval in outline, unite posteriorly with median notch; photophores anteriorly directed, numerous, small, arranged roughly in diagonal rows on mantle, head, and aboral surfaces of arms, more concentrated on ventral surfaces; buccal membrane 7-membered (except 6-membered in *H. bruuni*, *H. bonnellii bonnellii*, and *H. b. corpuscula*); inner web that connects arms vestigial to >60% of length of arms; suckers arranged in 2 rows on arms and usually in 5–8 rows on tentacular clubs.

REMARKS.—Histioteuthids occur worldwide from the Subarctic to the Subantarctic, from the surface to possibly 2000 m. Geographic distributions of species show varying degrees of association with slopes of continents, islands, and submarine mounts and ridges, with some species commonly found in open ocean. Diel vertical migration patterns appear to be widespread in the family. Histioteuthids often occur in large numbers and are known to be important in the diets of sperm and other toothed whales, certain seals, fishes, marine birds, and other squids. The family is composed of one genus and 13 currently recognized species/species groups. New information gathered by N. Voss, some of which is presented below, indicates a need for updating her 1969 monograph of the family.

The regions and provinces of the Atlantic referred to in the geographical distribution sections are those of Backus et al. (1977).

Histioteuthis Orbigny, 1841

GENERIC CHARACTERS.—Family is monotypic; generic characters are as given for family.

Key to Species and Subspecies of HISTIOTEUTHIDAE

(Adults, Subadults, and Juveniles >~10 mm ML*)

1. Median row of tubercles present on dorsal surfaces of mantle and basal portions of arms I–III (>~12–13 mm ML) 2
   No median row of tubercles on dorsal surfaces of mantle or basal portions of arms 5
2. Buccal membrane 6-membered . . . . . ***H. bruuni***
   Buccal membrane 7-membered 3
3. Photophores uniformly small, arranged in dense pattern on ventral surfaces of mantle and head; in 8–9 longitudinal rows on arms IV; in circlet of 19–21 around right eye . . . . . ***H. meleagroteuthis***
   Photophores uniformly moderately large, arranged in moderately dense pattern on ventral surfaces of mantle and head; in 5–6 longitudinal rows on arms IV; in circlet of 16 (rarely 17, 18) around right eye 4
4. Median row of tubercles <50% length of arms I–III and of mantle . . ***H. miranda***
   Median row of tubercles >60% length of arms I–III (>~12–17 mm ML; >50% at ~7–9 mm ML) and >50% length of mantle (>~12–17 mm ML) . . . ***H. oceani***
5. Single, enlarged, elongate photophore present on distal ends of arms I–III or I–IV; inner web deep (>50% length of longest arm in adults and subadults; ~19%–50% or greater in juveniles of ~10–20 mm ML; not known for juveniles of *H. bonnellii corpuscula*) 6
   Single, enlarged, elongate photophore not present on distal ends of arms; inner web vestigial to moderate in depth (<50% length of longest arms in adults and subadults; 0%–~26% in juveniles of ~10–20 mm ML) 8
6. Buccal membrane 7-membered . . . . . ***H. macrohista***
   Buccal membrane 6-membered 7
7. Single, enlarged, elongate photophore on distal ends of arms I–III; 17 large photophores around right eye; 2–3 conspicuous, large, round photophores present on left posteroventral margin of head (area of Southern Subtropical Convergence) . . . . . ***H. bonnellii corpuscula***†
   Single, enlarged, elongate photophore on distal ends of arms I–III or I–IV (seen at ~7 mm ML); 17 (?–16) large photophores around right eye; 2–4 conspicuous, large, round photophores may or may not be present on left posteroventral margin of head (north of Southern Subtropical Convergence in Atlantic and southeastern Indian Ocean; Mediterranean) . . . . . ***H. bonnellii bonnellii*** (group)

8. Photophores uniformly small, arranged in dense pattern on ventral surfaces of mantle and head; in 8–9 longitudinal rows on arms IV; in circlet of 18–21 around right eye . . . . . ***H. heteropsis***
   Photophores mostly large, arranged in less dense pattern on ventral surfaces of mantle and head; in 3–4 longitudinal rows on arms IV; in circlet of 17–18 around right eye 9
9. Distinct terminal group of photophores present on arms 10
   No distinct terminal group of photophores present on arms 12
10. Ventral surface of mantle with intermixed large and small photophores that occur to near anterior margin (seen at ~6 mm ML); dorsal pad of funnel organ with longitudinal median ridge on each lateral arm . . . . . ***H. atlantica*** (group)
    Ventral surface of mantle with uniformly large photophores on anterior $^{2}/_{3}$–$^{3}/_{4}$, posterior portion with abruptly reduced-size photophores; dorsal pad of funnel organ unsculptured 11
11. Rings of manus suckers of club with teeth confined to distal margins . . . . . ***H. celetaria celetaria***
    Rings of manus suckers of club with teeth around entire margins . . . . . ***H. celetaria pacifica***
12. Posterior $^{1}/_{3}$–$^{1}/_{2}$ of ventral surface of mantle and distal portions of arms IV with intermixed large, atypical, dark, oval photophores (seen in smallest known juvenile of 85 mm ML) . . . . . ***H. elongata*** (group)
    Large atypical photophores not present on mantle or arms 13
13. Dorsal pad of funnel organ with longitudinal median ridge on each lateral arm 14
    Dorsal pad of funnel organ unsculptured, surface may have swollen or deflated appearance 16
14. Posterior portions of median ridges on dorsal pad of funnel organ expanded into distinct flaps (seen at 7 mm ML); 17 large photophores in circlet around right eye . . . . . ***H. hoylei*** (group)
    Posterior portions of median ridges on dorsal pad of funnel organ not expanded into flaps; 17 large and 1 small photophore in circlet around right eye (at <~ 8 mm ML, small photophore usually lacking, but open space present) 15
15. Arms IV with 4 longitudinal rows of photophores, 3 of large organs (dorsalmost row with 5–8 organs), and 1 dorsal marginal row of small organs (marginal row usually not seen at <~15 mm ML) . . . . . ***H. reversa*** (group)
    Arms IV with 3 longitudinal rows of large photophores (dorsalmost row with 2–3 organs), no dorsal marginal row of small photophores . . . . . ***H. eltaninae***
16. Basal portions of arms IV with 4 rows of large photophores (northeastern Pacific) . . . . . ***H. corona berryi***†
    Basal portions of arms IV with 3 rows of large photophores 17
17. Fin length ~30%–40% length of mantle (at 34–52 mm ML); rings of large, median manus suckers of club with ~50–60 teeth (southeastern Pacific) . . . . . ***H. corona cerasina***†
    Fin length ~39%–55% length of mantle (at 32–55 mm ML); rings of large, median manus suckers of club with ~23–55 teeth 18
18. Fin length ~39%–47% length of mantle (at 32–55 mm ML; 49%–54% at 17–23 mm ML); rings of large, median manus suckers of club with ~33–55 teeth (Atlantic) . . . . . ***H. corona corona***
    Fin length ~46%–55% length of mantle (at 35–46 mm ML); rings of large, median manus suckers with ~23 teeth (northwestern Pacific) . . . . ***H. corona inermis***†

* In juveniles <~7–10 mm ML developing photophores often marked by overlying dark chromatophores.
† Poorly known.

Histioteuthis reversa (Verrill, 1880) (group)

SPECIES CHARACTERS.—*Young* (Figure 140): Ventral surface of mantle with intermixed large and small photophores (seen at 5 mm ML); basal portions of arms IV with 3 rows of large photophores and dorsal marginal row of small photophores (dorsal marginal row usually not seen in juveniles <~15 mm ML); 18 photophores (17 large and 1 small; occasionally 18 large and 1 small) around right eye (small photophore often not seen in juveniles <8 mm ML, but open space is present); dorsal pad of funnel organ with separate, longitudinal, median ridge on each lateral arm (sometimes seen as early as 9 mm ML); inner web low to vestigial.

Note: If distal ends of arms are in poor condition, denuded of photophores, this species may be confused with *H. atlantica* in the vicinity of the Southern Subtropical Convergence where the two species may co-occur. The two species can be separated by the development of the inner web, low to vestigial in *reversa*, and of medium depth in *atlantica*.

GEOGRAPHICAL DISTRIBUTION.—Widely distributed in North Atlantic Temperate Region including East and West Mediterranean; in western Atlantic extends into Subarctic to at least 52°N. Occurs in Mauritanean Upwelling, in Tropical Region east of the Lesser Antilles, and around South Africa in the Benguela and Agulhas currents. Two separately reported specimens from the southeastern Pacific between ~35°S-37°S and 74°W-83°W are probably misidentifications.

VERTICAL DISTRIBUTION.—Species occurs from surface waters to possibly below 1000 m. Closing nets have taken juveniles between ~100 m and 630 m during the day, and between 10 m and 260 m at night. Mature males and females have been taken in open nets fished at night at 600 m and 1300 m.

REMARKS.—May be composed of more than one species or subspecies. Abundance within geographic range is positively affected by proximity to land masses and submarine mounts and ridges. It is the commonest histioteuthid taken in Canadian Atlantic waters. Species matures at small to medium size (~49-100 mm ML).

REFERENCES.—N. Voss (1969, unpublished data), Nesis (1974), Lu and Clark (1975a, b), Retamal and Orellana (1977), Lea (1978), Lu and Roper (1979), Stephen (1982), Toll (1982).

Histioteuthis eltaninae N. Voss, 1969

SPECIES CHARACTERS.—*Young* (Figure 141): Ventral surface of mantle with intermixed large and small photophores from posterior end to near anterior margin; basal portions of arms IV with 3 rows of large photophores, dorsal row with only 2-3 organs; 18 photophores (17 large and 1 small) around right eye (small photophore lacking but open space present at ~7 mm ML); dorsal pad of funnel organ with longitudinal median ridge on each lateral arm; inner web low to vestigial.

GEOGRAPHICAL DISTRIBUTION.—Widespread in Subantarctic; probably circumglobal.

VERTICAL DISTRIBUTION.—Poorly known; extends from upper 100 m to unknown depths below 1000 m. Juveniles of 7-20 mm ML have been taken in open nets fished at night at 100-150 m, and during the day at 200 m.

REMARKS.—This is the commonest histioteuthid found in Subantarctic waters; most abundant in proximity to land and submarine ridges and mounts. Species matures at a small size (males at ~65-70 mm ML).

REFERENCES.—N. Voss (1969, unpublished data).

Histioteuthis elongata (N. Voss and G. Voss, 1962) (group)

SPECIES CHARACTERS.—*Young* (smallest known, 85 mm ML, with characters of species): Ventral surface of elongate mantle with intermixed large and small photophores from posterior end to near anterior margin, with additional intermixed large, dark, oval photophores on posterior $^1/_3$-$^1/_2$ of mantle; basal portions of arms IV with 3 rows of large photophores plus a dorsal marginal row of small photophores; distal portions of arms IV with large, dark, oval photophores; 18 photophores (17 large and 1 small) around right eye; each lateral arm of dorsal pad of funnel organ with longitudinal median ridge that appear to unite anteriorly; inner web low.

Eggs: Mature eggs (from oviduct) nearly round, ~2 mm diameter.

GEOGRAPHICAL DISTRIBUTION.—Poorly known; western North Atlantic between 30°N and 51°N; western Mediterranean; eastern Atlantic between 44°N and 13°S.

VERTICAL DISTRIBUTION.—Species occurs between surface and unknown depths below 1000 m. Known mostly from mature and near-mature animals that have been taken during the day with closing nets at 500-600 m and 800-1000 m, and at night on surface. Open nets have captured specimens at night at 0-570 m and 990-1010 m.

REMARKS.—May be composed of more than one species or subspecies. Species matures at medium to moderately large size (~87-195 mm ML) over broad geographic range.

REFERENCES.—N. Voss (1969, unpublished data), Lu and Roper (1979), Stephen (1982).

Histioteuthis atlantica (Hoyle, 1885) (group)

SPECIES CHARACTERS.—*Young* (Figure 142): Ventral surface of mantle with intermixed large and small photophores from posterior end to near anterior margin (seen at 6 mm ML); basal portions of arms IV with 3 rows of large photophores and a dorsal marginal row of intermixed medium and small photophores (last row to appear, the dorsal marginal row, can be partially seen at ~6 mm ML); terminal group of enlarged, dark photophores on arms I-III (1-3 terminal organs can be seen on arms I-III at ~6-13 mm ML; usually only overlying chromatophores are evident in juveniles <6 mm ML); 18 photophores (17 large and 1 small) around right eye; dorsal pad

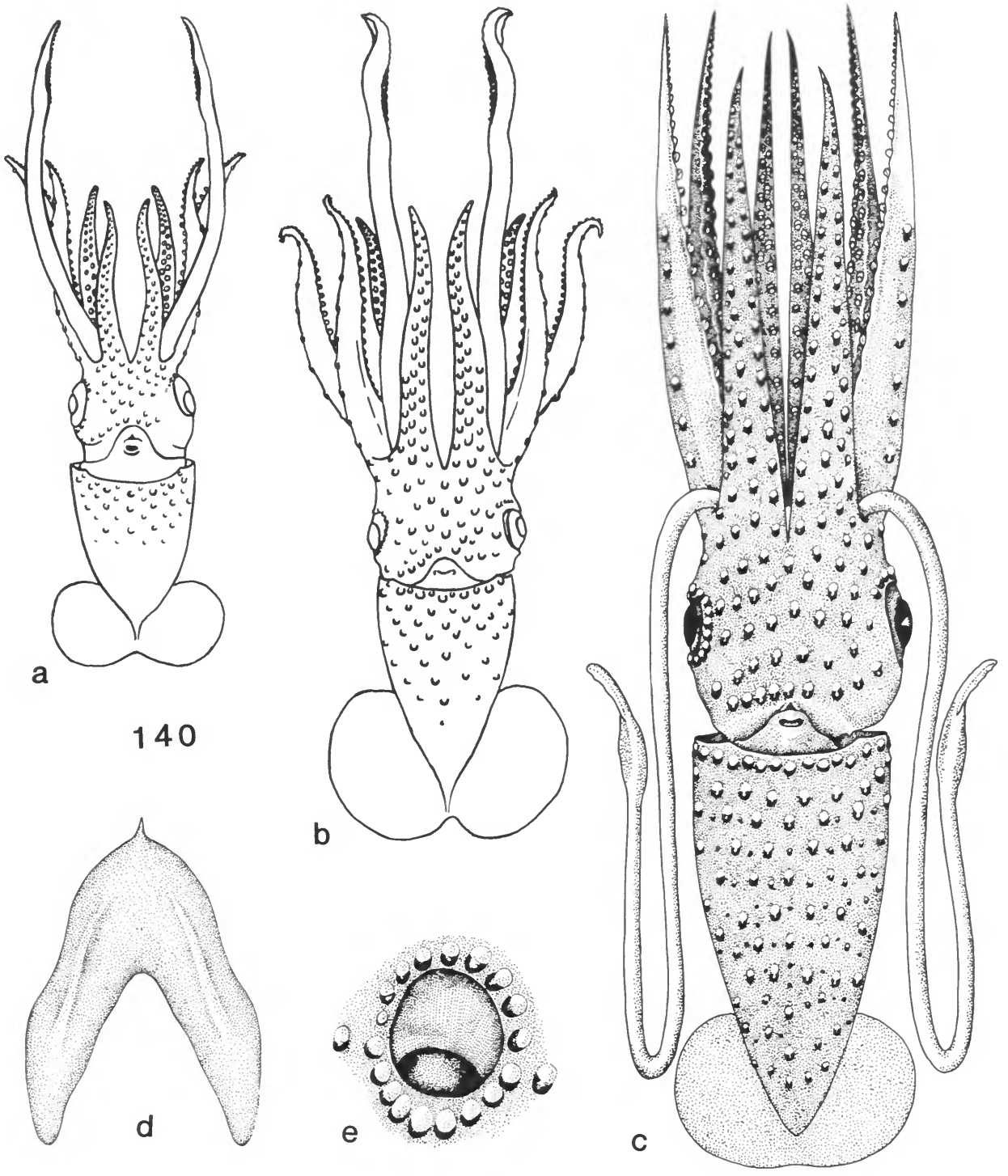
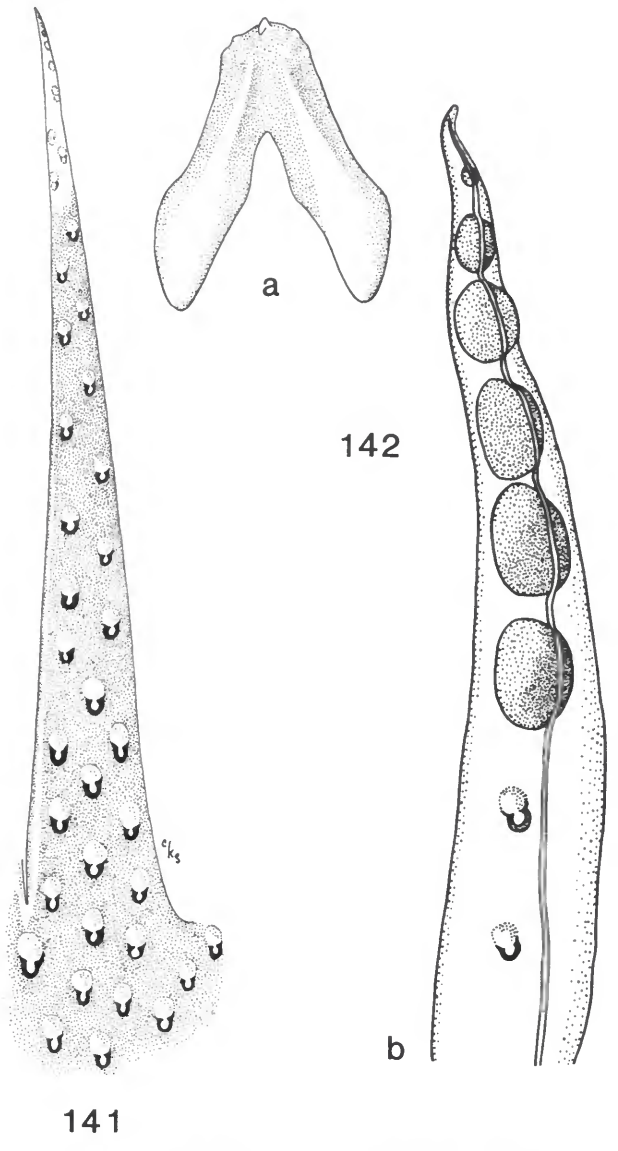


FIGURE 140.—*Histioteuthis reversa*, North Atlantic specimens: *a*, ventral view, 6 mm ML; *b*, ventral view, 9 mm ML; *c*, ventral view, 39 mm ML; *d*, dorsal pad of funnel organ of same; *e*, right eye, 29 mm ML (*a,b*, from N. Voss and G. Voss, 1962; *c–e*, from N. Voss, 1969).



FIGURES 141, 142.—Histioteuthidae: 141, *Histioteuthis eltaninae:* left arm IV, 53 mm ML. 142, *Histioteuthis atlantica,* 34 mm ML, southeastern Indian Ocean: *a,* dorsal pad of funnel organ; *b,* distal portion of arm I with terminal group of enlarged photophores. (From N. Voss, 1969.)

of funnel organ with longitudinal median ridge on each lateral arm (may be seen at ~11–15 mm ML); inner web moderately deep (low, but distinct, at ~8–10 mm ML).

Note: Juveniles that lack skin on distal ends of arms may be confused with *H. reversa,* but can be distinguished by the medium depth of the inner web, which is low to vestigial in *reversa.*

GEOGRAPHICAL DISTRIBUTION.—Circumglobal in Southern Subtropical Convergence and fringing waters, and in northern half of Subantarctic.

VERTICAL DISTRIBUTION.—Species has been taken in open nets fished at depths of 40–>2000 m. Small juveniles appear to be concentrated at night in upper 300 m. Mature males and females have been taken in open nets fished at various depths between 300 m and 2000 m at night, and between 900 m and 1000 m during the day.

REMARKS. May be comprised of more than one species or subspecies. This species matures at a small to medium size (~70–149 mm ML). The *Walther Herwig* took numerous mature males and maturing females in the mid-Atlantic portion of the Southern Subtropical Convergence and found this species to be the most common histioteuthid in central Atlantic waters of convergence. Species appears to spawn in open ocean.

REFERENCES.—N. Voss (1969, unpublished data), Nesis (1974, 1979).

Histioteuthis hoylei (Goodrich, 1896) (group)

SPECIES CHARACTERS.—*Young* (Figure 143): Ventral surface of mantle with approximately uniform, large photophores widely spaced on anterior 1/3–1/2, and with progressively smaller photophores on posterior portion (photophores formed only on anterior 1/2 of mantle at ~7 mm ML); 17 (sometimes 16) large photophores around right eye (seen at 7 mm ML); dorsal pad of funnel organ with longitudinal, median ridges that expand posteriorly into broad flaps on each lateral arm (flaps distinct at 7 mm ML); inner web low to vestigial; outer web may or may not be developed to ~12% of arm length in juveniles of 38 mm ML.

GEOGRAPHICAL DISTRIBUTION.—In Atlantic, species occurs in Gulf of Mexico, is widespread in Tropical and North Subtropical regions, and extends northward in western sector in Gulf Stream system to ~43°N; scarcely caught, and distribution poorly known, in South Subtropical Region. Species is widespread in Indian Ocean between 10°N and Southern Subtropical Convergence, and in Pacific in equatorial, tropical, and subtropical waters.

VERTICAL DISTRIBUTION.—Captures with open and with closing nets indicate that juveniles and subadults range during the day from ~375–850 m, and at night from ~50–500 m, with larger animals tending to be slightly deeper than smaller ones during both periods. Near-mature and mature animals appear to range to >1000 m.

REMARKS.—Composed of more than one species or subspecies. Material in recent literature referred to *Histioteuthis dofleini* (Pfeffer, 1912) belongs to this species. The long-lost type of Goodrich's species, a juvenile of 22 mm ML from the Indian Ocean, recently located in the collections of the National Museum of Wales by C. Roper, was examined by N. Voss and

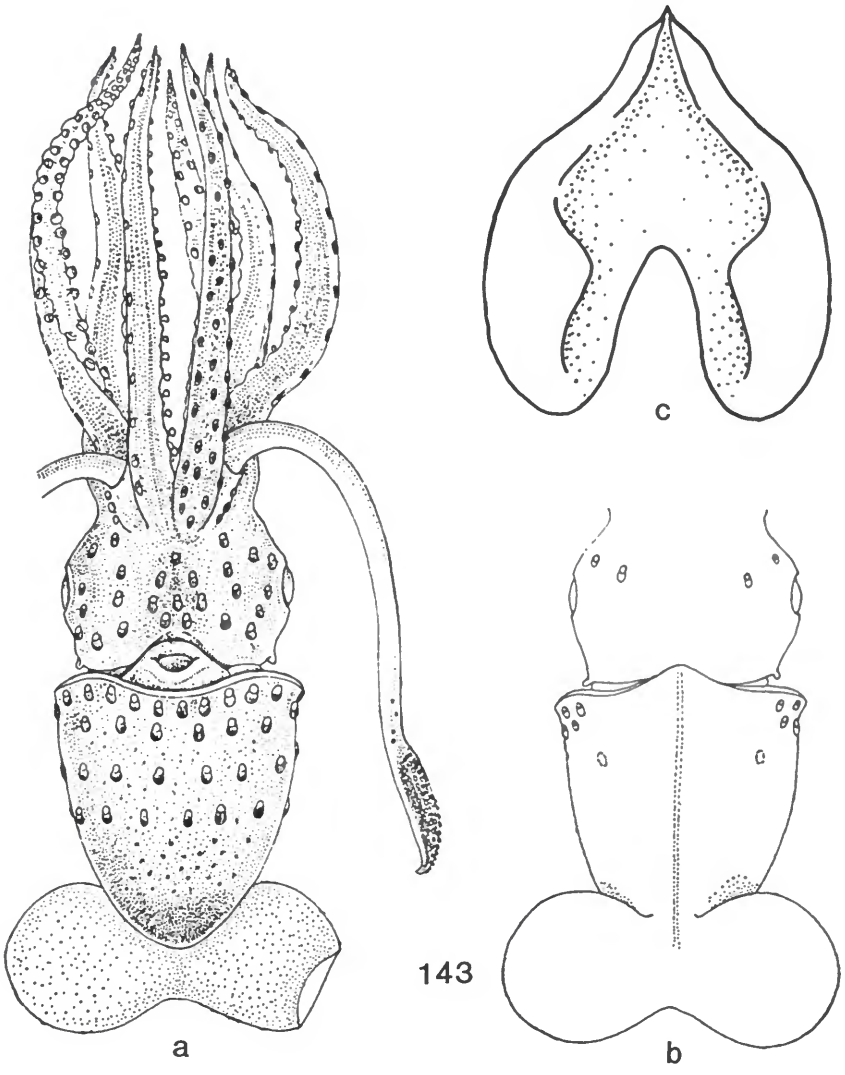


FIGURE 143.—*Histioteuthis hoylei* (*a,b,* ~8 mm ML, California Current; *c,* 8 mm ML, North Atlantic, USNM 727033): *a,* ventral view (original drawing); *b,* dorsal view (from Okutani and McGowan, 1969); *c,* dorsal pad of funnel organ (original drawing).

found to be identical to *dofleini*. By principal of priority, *hoylei* (Goodrich, 1896) becomes the valid name for this species. This squid matures at a small to large size (~72- >210 mm ML), and is commonly found in open ocean as well as in close proximity with land and submarine ridges and mounts. It is common in the northwestern Pacific, where it is a major item in the diets of sperm whales. It is the only histioteuthid commonly caught in the northern Sargasso Sea. Over its currently recognized "cosmopolitan distribution," the species displays considerable variation in a number of morphological characters (see N. Voss, 1969).

REFERENCES.—N. Voss (1969, unpublished data), Clarke and Lu (1975), Roper and Young (1975), Young (1975), Okutani et al. (1976), Stephen (1982), Lea (1978, 1984).

Histioteuthis celetaria celetaria (G. Voss, 1960)

SPECIES CHARACTERS.—*Young* (>~10 mm ML) (Figure 144*a–c*): 17 large photophores around right eye; ventral surface of mantle with uniformly large photophores on anterior $^2/_3$–$^3/_4$ and posterior portion with abruptly reduced-size photophores; basal portions of arms IV with 3 rows of

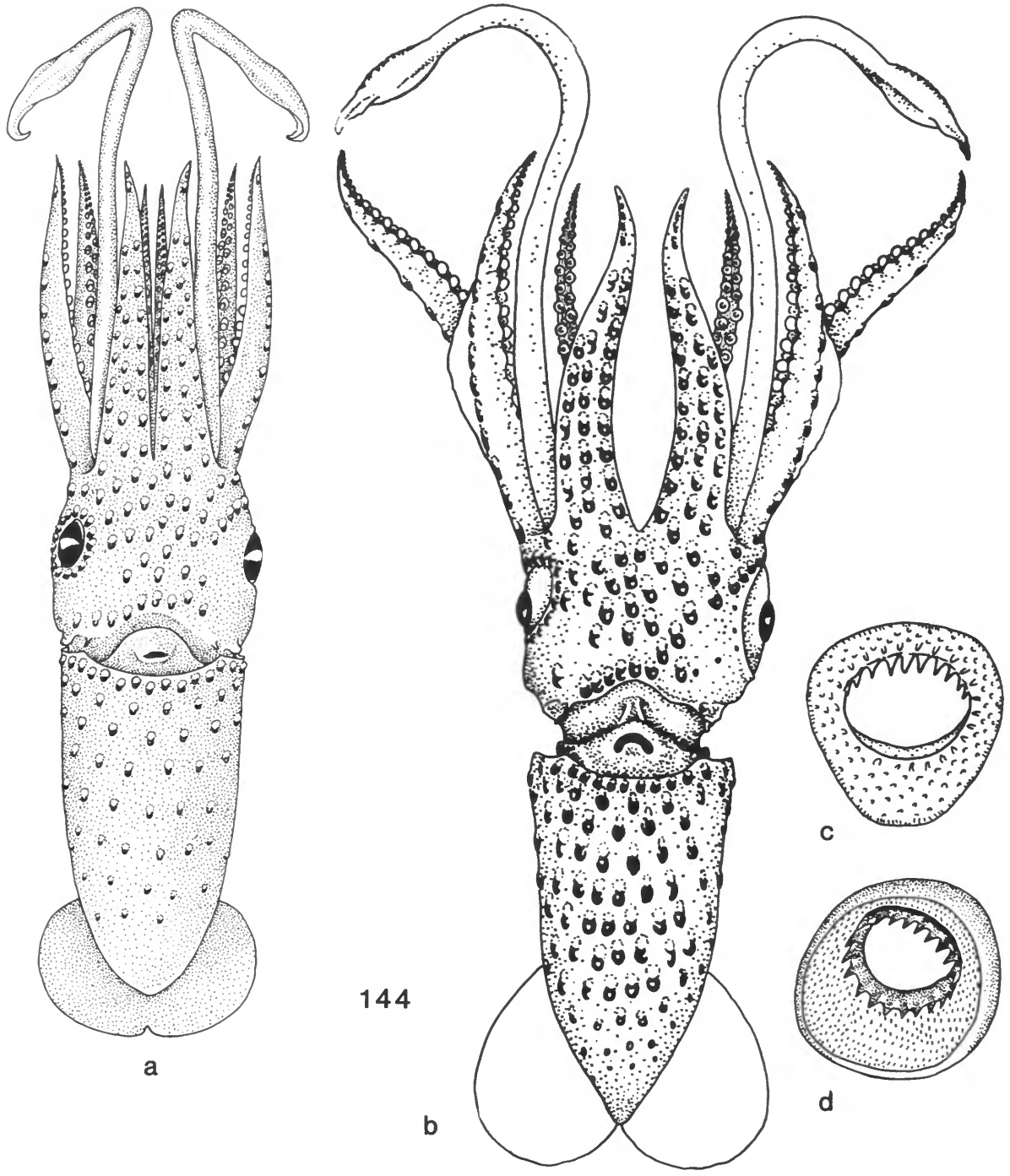


FIGURE 144.—*a–c, Histioteuthis celetaria celetaria*, North Atlantic: *a*, ventral view, 10 mm ML; *b*, ventral view, 39 mm ML; *c*, manus sucker from ventral row of same. *d, Histioteuthis celetaria pacifica:* manus sucker from ventral row, 74 mm ML, southwestern Indian Ocean (*a,d*, from N. Voss, 1969; *b,c*, from G. Voss, 1960).

photophores; arms I–IV with terminal group of photophores (usually seen at ~10–39 mm ML); ventral marginal suckers on manus of club with shelf-like expansion of denticulate collar; rings of manus suckers of club with teeth confined to distal margins; photophores reduced in number or lacking on ventral posterolateral surface of head suggesting well-defined "window" areas.

GEOGRAPHICAL DISTRIBUTION.—Poorly known from 6 captures widely scattered in Tropical and both Subtropical regions of Atlantic.

VERTICAL DISTRIBUTION.—Known only from open net captures of juveniles in upper 40 m to 820 m.

REFERENCES.—N. Voss (1969, unpublished data), Nesis (1974), Stephen (1982).

Histioteuthis celetaria pacifica (G. Voss, 1962)

SPECIES CHARACTERS.—*Young* (>~10 mm ML) (Figure 144*d*): 17 (sometimes 16) large photophores around right eye; ventral surface of mantle with uniformly large photophores on anterior $^{2}/_{3}$–$^{3}/_{4}$, and posterior portion with abruptly reduced-size photophores; basal portions of arms IV with 3 rows of photophores; arms I–IV with terminal group of photophores; ventral marginal suckers on manus of club with shelf-like expansion of denticulate collar; rings of manus suckers of club with teeth around entire margins; photophores reduced in number on ventral posterolateral surface of head suggesting moderately to poorly defined "window" areas.

GEOGRAPHICAL DISTRIBUTION.—In Pacific, widespread in equatorial and both tropical regions, from Hawaii, and Indo-Pacific. In Indian Ocean known from off northwestern Australia (abundant) and off Madagasgar.

VERTICAL DISTRIBUTION.—Known to range between surface and ~800 m. Closing nets captured juveniles of ~20–30 mm ML at night between ~250 m and 400 m, and a 60 mm ML specimen during the day at 550 m. A 32 mm ML juvenile was taken at night on surface. Near-mature and mature adults have been taken with open nets at night in midwater at 750–760 m and on continental slopes between 400 m and 600 m.

REMARKS.—Geographical distribution largely associated with land masses. Species matures at small to medium size (~65–>122 mm ML). Species appears to spawn in large aggregations on continental slopes.

REFERENCES.—N. Voss (1969, unpublished data), Young (1978), S. Slack-Smith (unpublished data).

Histioteuthis corona corona (N. Voss and G. Voss, 1962)

SPECIES CHARACTERS.—*Young* (Figure 145): Ventral surface of mantle with numerous, uniformly large photophores on anterior $^{1}/_{2}$, progressively smaller photophores on posterior $^{1}/_{2}$; 17 (sometimes 16) large photophores around right eye; inner web moderately developed (~15%–23% of longest arm at ~36–55 mm ML); dorsal pad of funnel organ unsculptured,

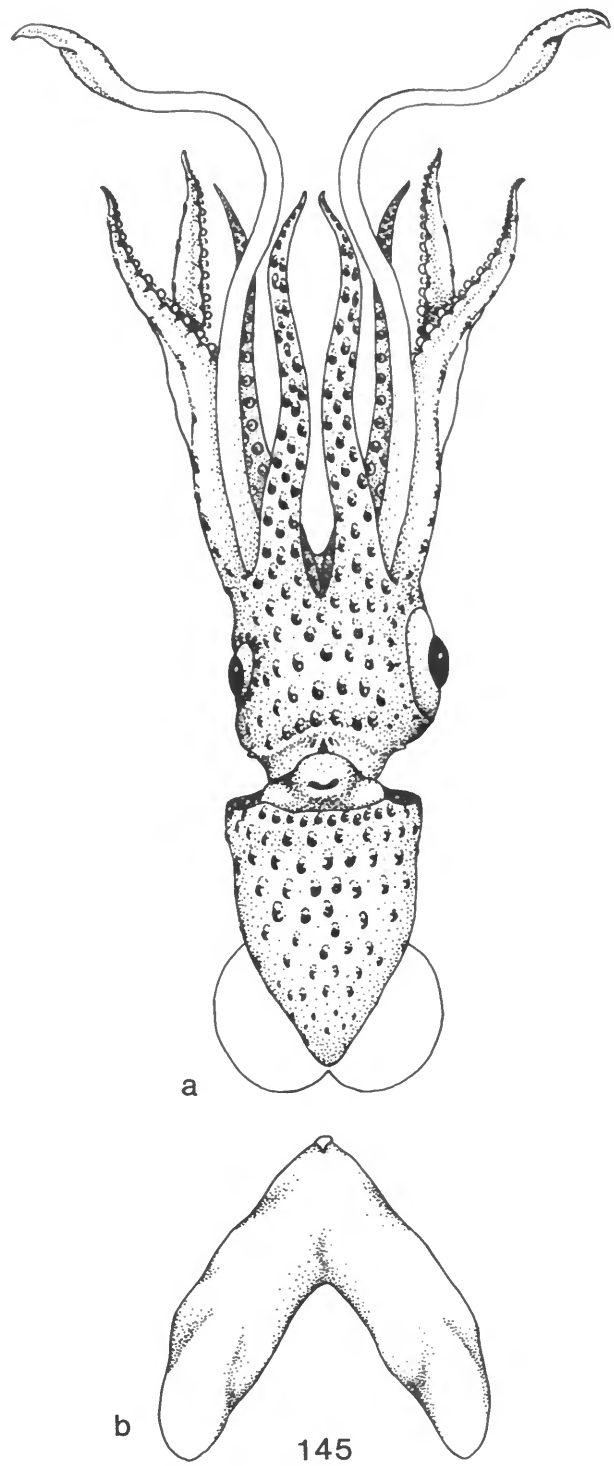


FIGURE 145.—*Histioteuthis corona corona*, 33 mm ML female, Gulf of Mexico: *a*, ventral view; *b*, dorsal pad of funnel organ (from N. Voss and G. Voss, 1962).

often appears swollen or deflated; basal portions of arms IV with 3 rows of large photophores; fin length ~49%–54% length of mantle at ~17–23 mm ML, 39%–47% at ~32–55 mm ML; rings of large, median manus suckers of club with ~33–35 pointed teeth around entire margins.

GEOGRAPHICAL DISTRIBUTION.—Gulf of Mexico; tropical Atlantic region; scattered northward in western Atlantic in Gulf Stream system to ~42°N. In eastern Atlantic extends from ~35°N southward to Southern Subtropical Convergence; scattered around South Africa in Benguela and Agulhas currents into southwestern Indian Ocean.

VERTICAL DISTRIBUTION. Range extends from ~200 m to unknown depths below 1000 m; seldom caught in upper 200 m. Juveniles of 7–21 mm ML have been taken in closing nets during the day between 410 and 700 m, and at night between 200 and 500 m.

REMARKS.—Distribution is associated with land masses. Species matures at medium to moderately large size (males at ~110–170 mm ML).

REFERENCES.—N. Voss (1969, unpublished data), Clarke and Lu (1974, 1975), Stephen (1982).

Histioteuthis corona berryi N. Voss, 1969

SPECIES CHARACTERS.—*Young* (Figure 146): Ventral surface of mantle with numerous, uniformly large photophores on anterior 1/2, progressively smaller photophores on posterior 1/2; 17 large photophores around right eye; inner web moderately developed (~15%–23% of longest arm at ~36–55 mm ML); dorsal pad of funnel organ unsculptured, often appears swollen or deflated; basal portions of arms IV with 4 rows of large photophores; fins ~40%–44% ML in juveniles of 35–36 mm ML; rings of large, median manus suckers of club with ~28–34 teeth around entire margins.

GEOGRAPHICAL DISTRIBUTION.—Poorly known from only 4 specimens, all taken in California Current between 26°N and 30°N, 115°W and 126°W; appears to be uncommon in current.

VERTICAL DISTRIBUTION.—Has been taken in open nets fished at 300 m to depths of ~750 m. Smallest known juvenile, 35 mm ML, taken at night at ~300 m.

REFERENCES.—N. Voss (1969, unpublished data).

Histioteuthis corona cerasina Nesis, 1971

SPECIES CHARACTERS.—*Young* (Figure 147): Ventral surface of mantle with numerous, uniformly large photophores on anterior 1/2, progressively smaller photophores on posterior 1/2; 17 large photophores around right eye; inner web moderately developed (~15%–23% of longest arm at ~36–55 mm ML); dorsal pad of funnel organ unsculptured, often appears swollen or deflated; basal portions of arms IV with 3 rows of large photophores; fin length ~30%–40% length of mantle at ~34–52 mm ML; rings of large, median manus suckers of club with ~50–60 pointed teeth around entire margins.

GEOGRAPHICAL DISTRIBUTION.—Poorly known; Eastern South Pacific between 00° and 24°S (may extend to ~37°S), 71°W and 85°W in the Peru-Chile Current.

VERTICAL DISTRIBUTION.—Has been taken in open nets fished at 200 m to depths of 1500 m.

REFERENCES.—Nesis (1971), Retamal and Orellana (1977), N. Voss (1969, unpublished data).

Histioteuthis corona inermis (Taki, 1964)

SPECIES CHARACTERS.—*Young:* Ventral surface of mantle with numerous, uniformly large photophores on anterior 1/2, progressively smaller photophores on posterior 1/2; 17 (sometimes 16) large photophores around right eye; inner web moderately developed; dorsal pad of funnel organ unsculptured, often appears swollen or deflated; basal portions of arms IV with 3 rows of large photophores; fin length ~46%–55% of length of mantle at ~35–46 mm ML; rings of large, median manus suckers of club with ~20–23 teeth around entire margins.

GEOGRAPHICAL DISTRIBUTION.—Western North Pacific; known only from Suruga Bay and Tosa Bay, Japan.

REFERENCES.—Taki (1964), Okutani et al. (1987).

Histioteuthis miranda (Berry, 1918)

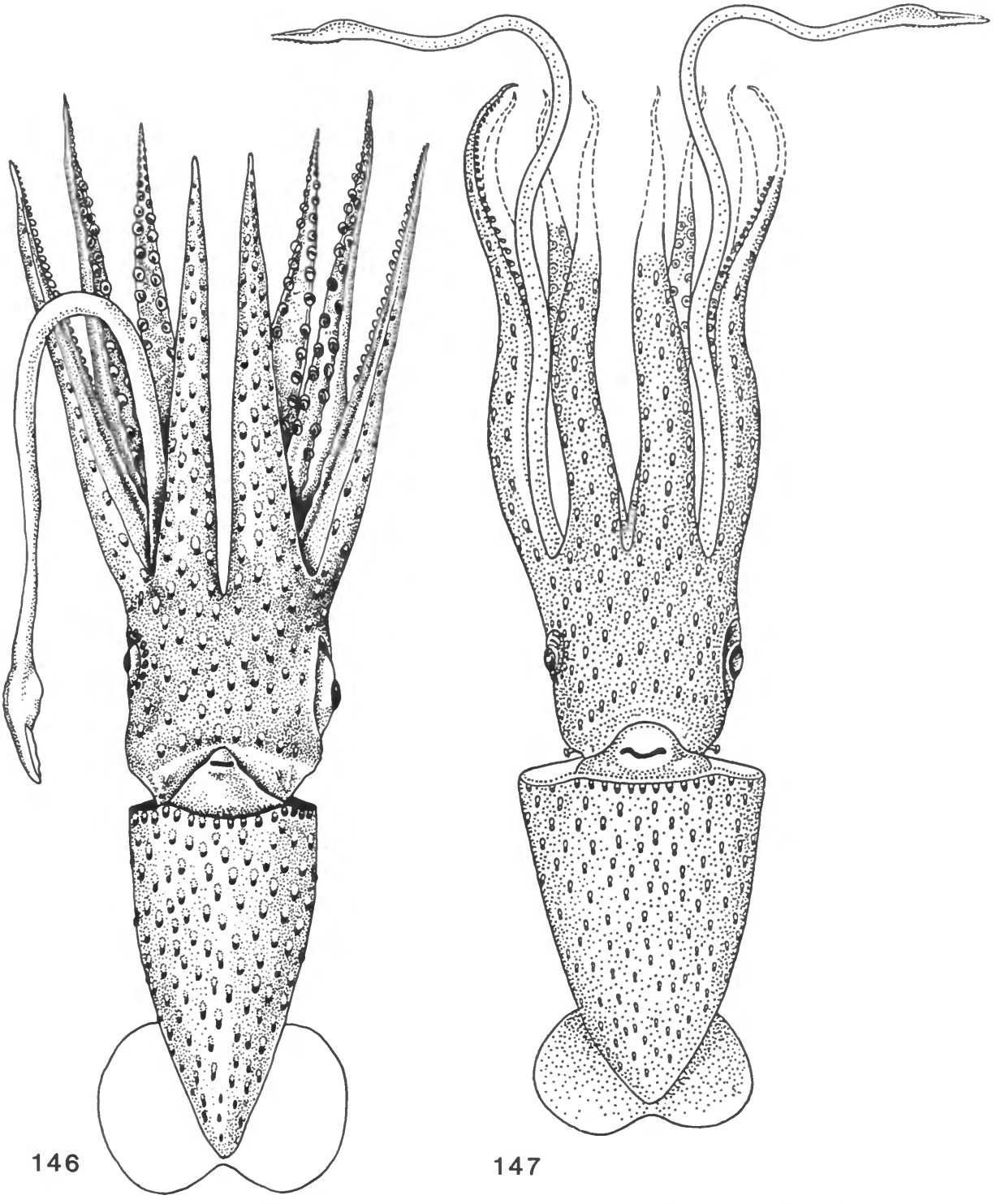
SPECIES CHARACTERS.—*Young* (Figure 148): Arms I–III and dorsum of mantle with median row of tubercles (rows <50% of lengths of arms I–III, and <50% length of mantle at ~13–38 mm ML); ventral surfaces of mantle and head with numerous, nearly uniform, moderately large photophores arranged in moderately dense pattern; basal portions of arms IV with 5 rows of photophores; 16 (rarely 17) uniform-size photophores around right eye; inner web moderately deep.

GEOGRAPHICAL DISTRIBUTION.—Southern Subtropical Convergence (probably circumglobal, but at present unreported from east or west coasts of South America), extending northward in boundary currents and in vicinity of New Zealand.

VERTICAL DISTRIBUTION.—Known to range from subsurface waters to 1000 m. Open net tows at night have captured juveniles of 15–17 mm ML at 49 m (in scattering layer) and 600 m, and large juveniles of 47–92 mm ML between 300 m and 600 m. Subadults and adults have been taken during the day on or near the bottom between 600 m and 1000 m.

REMARKS.—Species matures at a moderately large to large size (~160–>250 mm ML). It is an important item in the diet of toothed whales. Distribution is closely associated with land masses. Species appears to spawn in large aggregations on continental and island slopes. Numerous mature males and near-mature females have been taken at 700–1000 m during the day on the slopes of South Africa and Madagascar between 25°S and 35°S, 17°E and 36°E. Adults also have been taken in large numbers on the slopes off Tasmania.

REFERENCES.—N. Voss (1969, unpublished data), Clarke (1980), C.C. Lu (unpublished data).



FIGURES 146, 147.—Histioteuthidae: 146, *Histioteuthis corona berryi:* ventral view, 47 mm ML, holotype (from N. Voss, 1969). 147, *Histioteuthis corona cerasina:* ventral view, 48 mm ML (from Nesis, 1971).

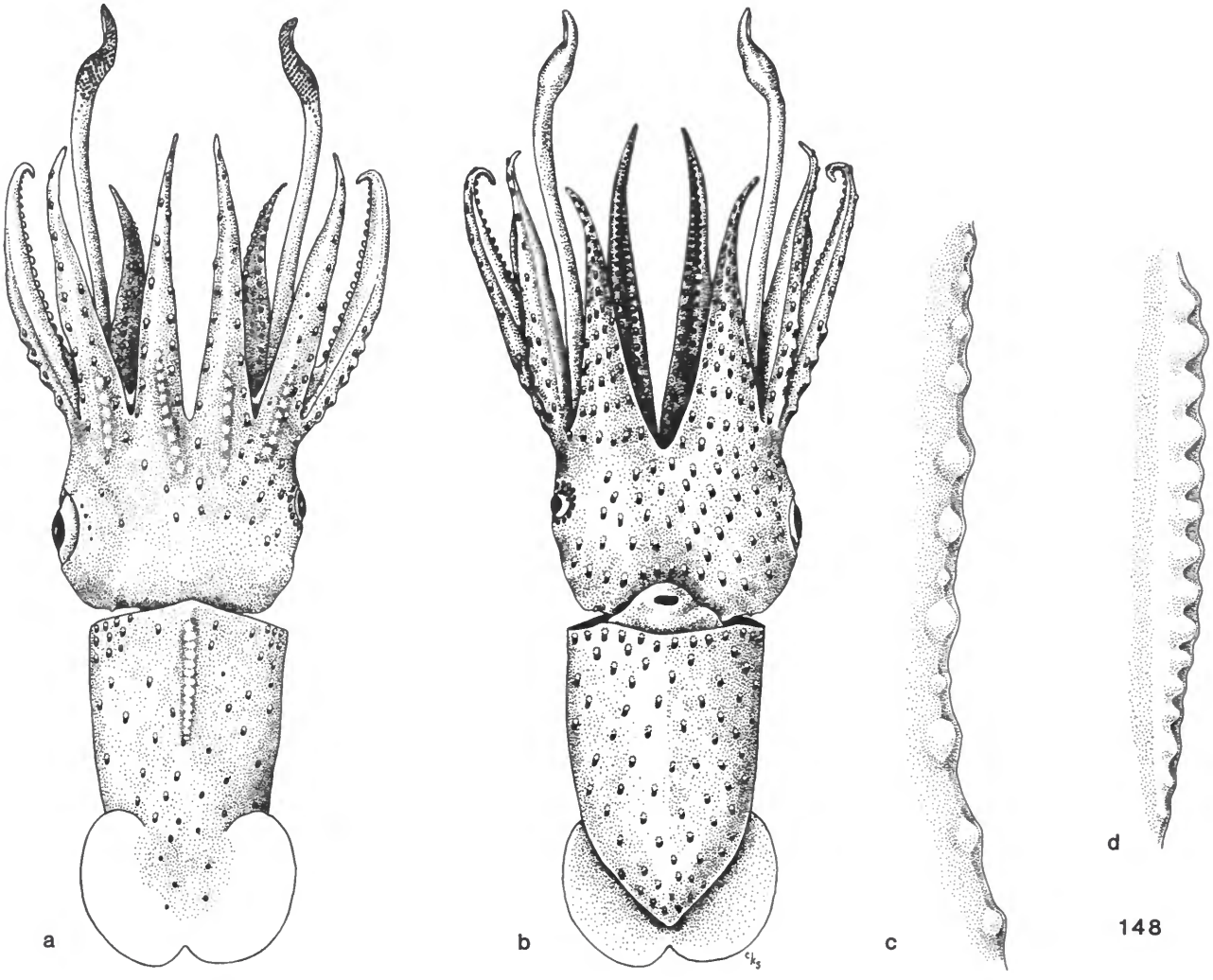


FIGURE 148.—*Histioteuthis miranda*, 17 mm ML, 32°S, 174°E: *a*, dorsal view; *b*, ventral view; *c*, lateral view of tubercles on left arm I; *d*, lateral view of tubercles on dorsum of mantle. (From N. Voss, 1969.)

Histioteuthis oceani (Robson, 1948)

SPECIES CHARACTERS.—*Young* (Figure 149): Arms I–III and dorsum of mantle with median row of tubercles (rows >60% length of arms I–III and >50% length of mantle at ~12–17 mm ML; at ~7–8 mm ML, tubercular rows >50% length of arms I–III); ventral surface of mantle with numerous, approximately uniform, moderately large photophores arranged in moderately dense pattern; basal portions of arms IV with 5–6 rows of photophores (can be seen at 7–8 mm ML); 16 (rarely 18) photophores around right eye; inner web moderately deep.

GEOGRAPHICAL DISTRIBUTION.—Poorly known; has been taken in Indo-Pacific, and widely distributed in Pacific equatorial, and north tropical and subtropical waters to ~28°N north of Hawaii.

VERTICAL DISTRIBUTION.—The species has been captured in nets fished at depths from the upper 170 m to 845 m. Juveniles <23 mm ML have been taken during the day between 300 m and ~550 m, and at night between the surface and 180 m. Large juveniles, subadults, and adults have been taken during the day at ~700 m and 845 m, and at night between ~275 m and 700 m. A mature male was captured at night at 600–700 m.

REMARKS.—N. Voss recently examined Robson's unique type, a 7.2 mm ML juvenile from the Galapagos (deposited in the British Museum (Natural History)), and found it to possess

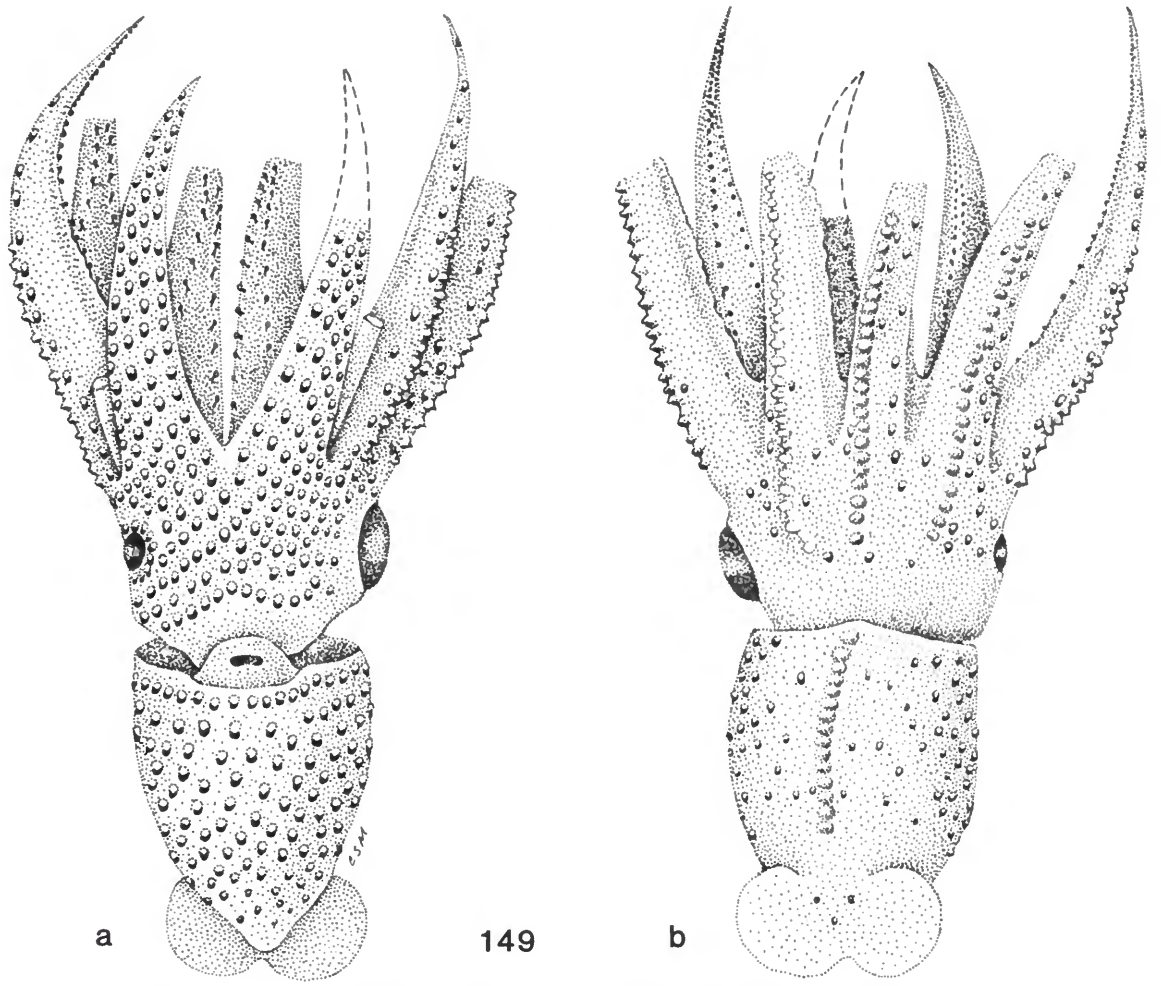


FIGURE 149.—*Histioteuthis oceani*, 12 mm ML, Hawaiian waters: *a*, ventral view; *b*, dorsal view (C. McSweeny, unpublished data).

several important, undescribed characters, including details of the photophore pattern and the presence of long median rows of tubercles on arms I–III. She determined the type to be identical to a 17 mm ML specimen from the Philippines misidentified by her (1969) as *H. miranda*, to three specimens misidentified to *H. miranda* by Okutani (1974:66), to material from Hawaii reported by Young (1978) as *Histioteuthis* sp., and to unpublished specimens from Hawaii and the Celebes Sea. This species matures at a small size (males at ~50 mm ML). Except for size, it closely resembles *H. miranda*. Distribution appears to be associated with island masses and submarine rises.

REFERENCES.—N. Voss (1969, Philippine specimen reported as *H. miranda*, unpublished data), Okutani (1974, reported as *H. miranda*), Young (1978, reported as *Histioteuthis* sp.).

Histioteuthis meleagroteuthis (Chun, 1910)

SPECIES CHARACTERS.—*Young* (Figures 150, 151): Arms I–III and dorsum of mantle with median row of tubercles (can be seen in juveniles as small as 13 mm ML); ventral surfaces of mantle and head with dense pattern of small photophores (seen at 9 mm ML); basal portions of arms IV with 8–9 rows of photophores; 19–21 photophores around right eye; moderately deep inner web (appears only as trace in juveniles <20 mm ML).

Note: In the eastern Pacific, juveniles <~12 mm ML may be confused with *H. heteropsis*, which inhabits waters to the north and south of the range of *meleagroteuthis*.

GEOGRAPHICAL DISTRIBUTION.—Widely distributed in Atlantic in North Subtropical and Tropical regions and Maurita-

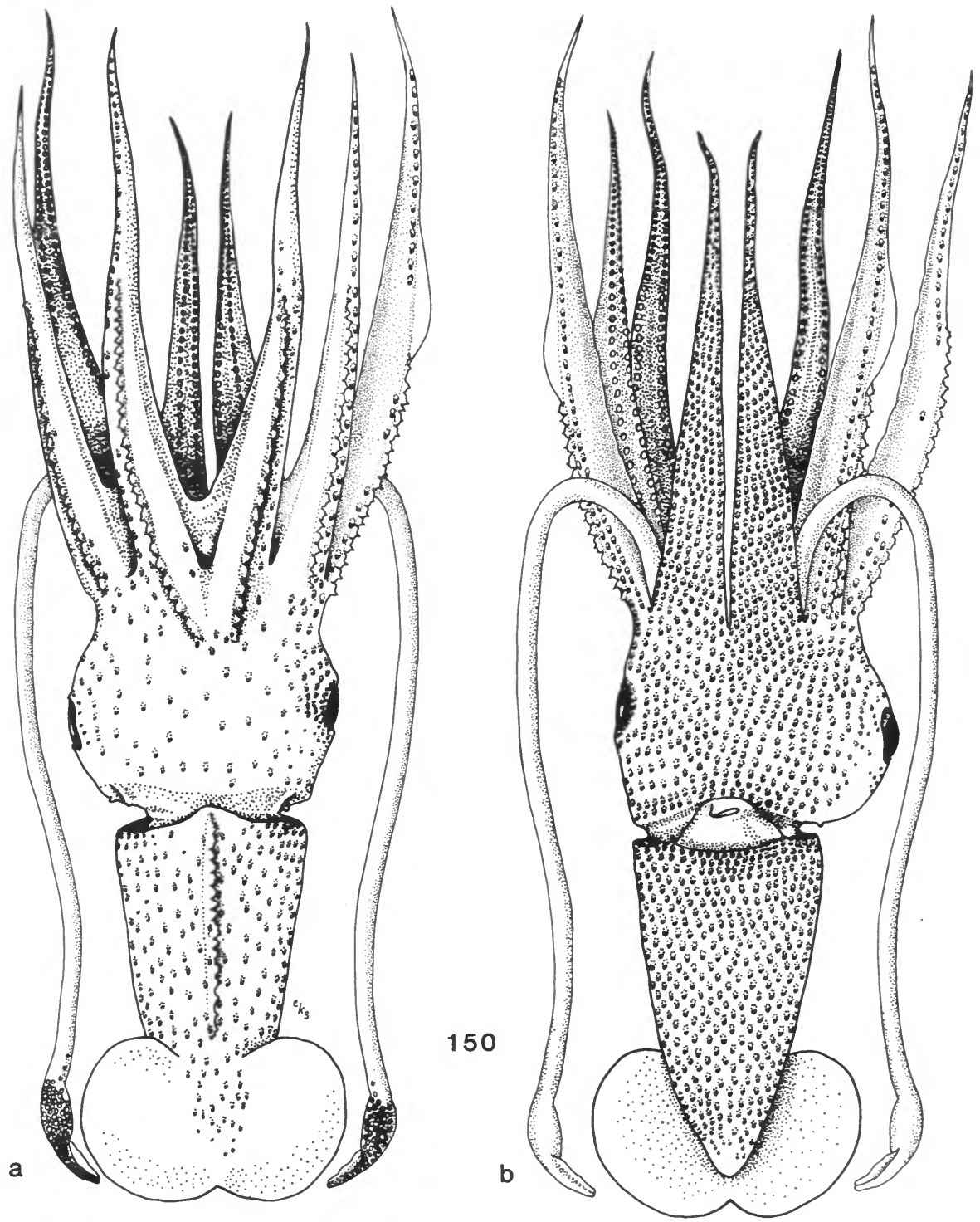
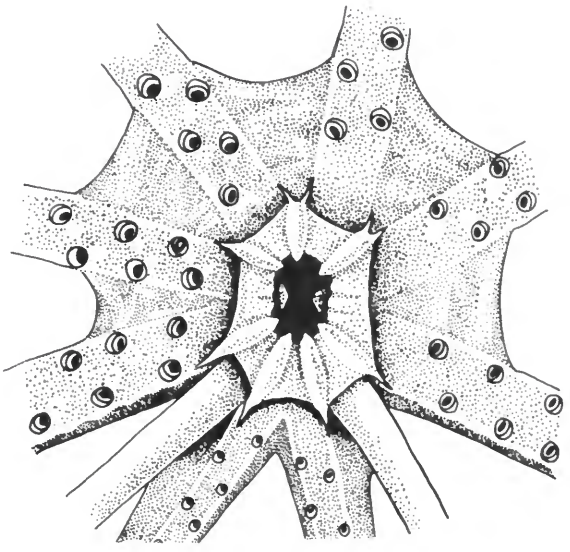


FIGURE 150.—*Histioteuthis meleagroteuthis*, 48 mm ML, Southwestern Pacific, neotype: *a*, dorsal view; *b*, ventral view. (From N. Voss, 1969.)



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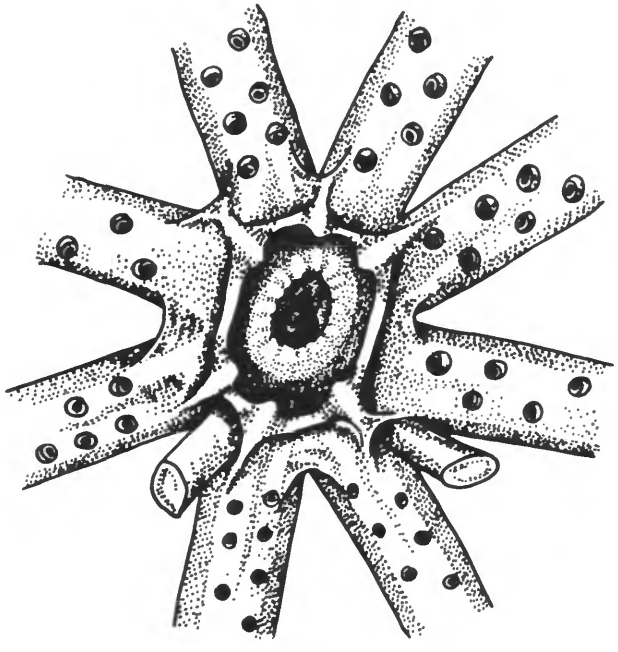

152

FIGURES 151, 152.—Histioteuthidae: 151, *Histioteuthis meleagroteuthis:* buccal view with 7-membered buccal membrane, 48 mm ML, Southwestern Pacific, neotype. 152, *Histioteuthis bruuni:* buccal view with 6-membered membrane, 80 mm ML, holotype. (From N. Voss, 1969.)

nean Upwelling (*Walther Herwig* found relatively high abundance over range in eastern Atlantic); not reported from South Subtropical Region. Widely distributed in Indian Ocean in equatorial waters south to Southern Subtropical Convergence, in Indo-Pacific, and in western Pacific between subtropical convergences. Species occurs in considerable abundance in areas of Kurosio Current. In eastern Pacific, species appears to be confined to equatorial waters.

VERTICAL DISTRIBUTION.—Species appears to range between upper 65 m to >1000 m. Closing nets have captured juveniles <10 mm ML during the day at 210–3000 m, and juveniles of 10–20 mm ML at 690 m. Nighttime captures of juveniles of 20–30 mm ML were made at 100–200 m and 360 m. Mature animals were taken with open nets fished at night at 910–1010 m.

REMARKS.—This species matures at a small size (~65–80 mm ML); its geographic distribution shows association with land masses and submarine ridges and mounts. Over the currently recognized, circumglobal distribution of this species, some unreported variations in the attachments (but not the number of lappets) of the buccal membrane have been found by N. Voss. The significance of these variations can be determined only by future, detailed study.

REFERENCES.—N. Voss (1969, unpublished data), Okutani (1974), Clarke and Lu (1975), Roper and Young (1975).

Histioteuthis bruuni N. Voss, 1969

SPECIES CHARACTERS.—*Young* (not known; characters given assumed from solely described specimen, a mature male; Figure 152): Arms I–III and dorsum of mantle with median row of tubercles; arms IV and ventral surfaces of mantle and head assumed (on basis of photophore pattern on remaining few pieces of skin) to have dense pattern of small photophores; ~20 uniformly small photophores around right eye; inner web appears to be of moderate depth; 6-membered buccal membrane.

GEOGRAPHICAL DISTRIBUTION.—Known only from holotype and a recently reported, but undescribed, male of 63 mm ML, both from the southeastern Atlantic between 23°S and 34°S, 2°E and 4°E.

VERTICAL DISTRIBUTION.—Two known specimens taken in open nets fished at 960–1080 m and at ~3000 m (mature male).

REMARKS.—A detailed study of the new specimen, together with the holotype and the considerably large, unstudied collections now available of *meleagroteuthis*, a species that *bruuni* closely resembles, may show whether *bruuni* is a valid species or a variant of *meleagroteuthis* as has been recently suspected.

REFERENCES.—N. Voss (1969), Nesis and Nikitina (1986).

Histioteuthis heteropsis (Berry, 1913)

SPECIES CHARACTERS.—*Young* (Figure 153): Ventral surfaces of mantle and head with dense pattern of small photophores; basal portions of arms IV with 8–9 rows of

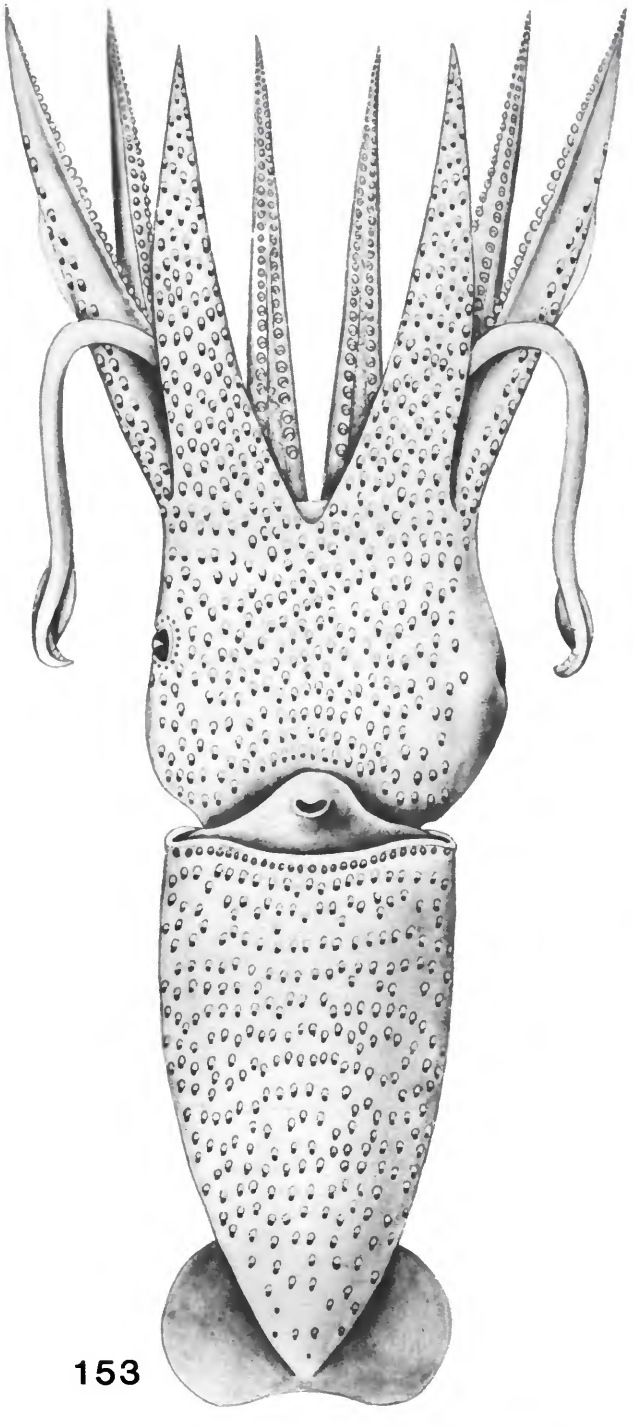

FIGURE 153.—*Histioteuthis heteropsis:* ventral view, 35 mm ML, California Current. (From Young, 1972.)

photophores; 19–20 (sometimes 18 or 21) photophores around right eye; no median rows of tubercles on arms or dorsum of mantle.

Note: Juveniles <~13 mm ML may be confused with *H. meleagroteuthis,* which occurs in the eastern tropical Pacific.

GEOGRAPHICAL DISTRIBUTION.—Known only from eastern Pacific where species appears to be antitropical in distribution; common histioteuthid in California Current between ~27°N and 37°N, and in Peru-Chile Current between ~30°S and 36°S. A single specimen has been reported from equatorial waters.

VERTICAL DISTRIBUTION.—Open-net captures show species to occur during the day between ~300 m and 800 m, with greatest concentration between 500 m and 700 m, and at night between the surface and ~400 m, with greatest concentration between 300 m and 400 m. Night hauls in upper 200 m took only juveniles <20 mm ML.

REMARKS.—A small species with males mature at ~54–89 mm ML.

REFERENCES.—Okutani and McGowan (1969, in part), N. Voss (1969, unpublished data), Young (1972), Nesis (1973), Roper and Young (1975), Retamal and Orellana (1977).

Histioteuthis macrohista N. Voss, 1969

SPECIES CHARACTERS.—*Young* (Figure 154): Inner web between arms I–III deep (~18%–29% of arm length at 8–10 mm ML, ~26%–50% at 10–20 mm ML); single, enlarged, elongate, terminal photophore on arms I–III (seen in juveniles as small as 7.2 mm ML); unique 7-membered buccal membrane pattern.

GEOGRAPHICAL DISTRIBUTION.—Circumglobal in Southern Subtropical Convergence and fringing waters; north in Benguela Current to ~27°S.

VERTICAL DISTRIBUTION.—Appears to range from surface to >1000 m. All captures have been taken with open nets. Shallowest hauls to capture juveniles at night fished between 97 m and 110 m, and during the day between 725 m and 800 m.

REMARKS.—A small species maturing at ~40–55 mm ML. Commonly occurs and may spawn in open ocean. Mature animals have been taken over a broad stretch of the open Atlantic at night in open nets at 100 m, 316–328 m, and 600–610 m.

REFERENCES.—N. Voss (1969, unpublished data), Nesis (1974).

Histioteuthis bonnellii bonnellii (Ferussac, 1835) (group)

SPECIES CHARACTERS.—*Young* (Figure 155): Inner web between arms I–III deep (~16%–37% of length of longest arm at 8–10 mm ML, ~19%–58% at >10–20 mm ML); single enlarged, elongate terminal photophore on arms I–III or I–IV (seen in juveniles as small as 7 mm ML; at 15–20 mm ML, photophore measures ~12%–15% of length of arm); 6-

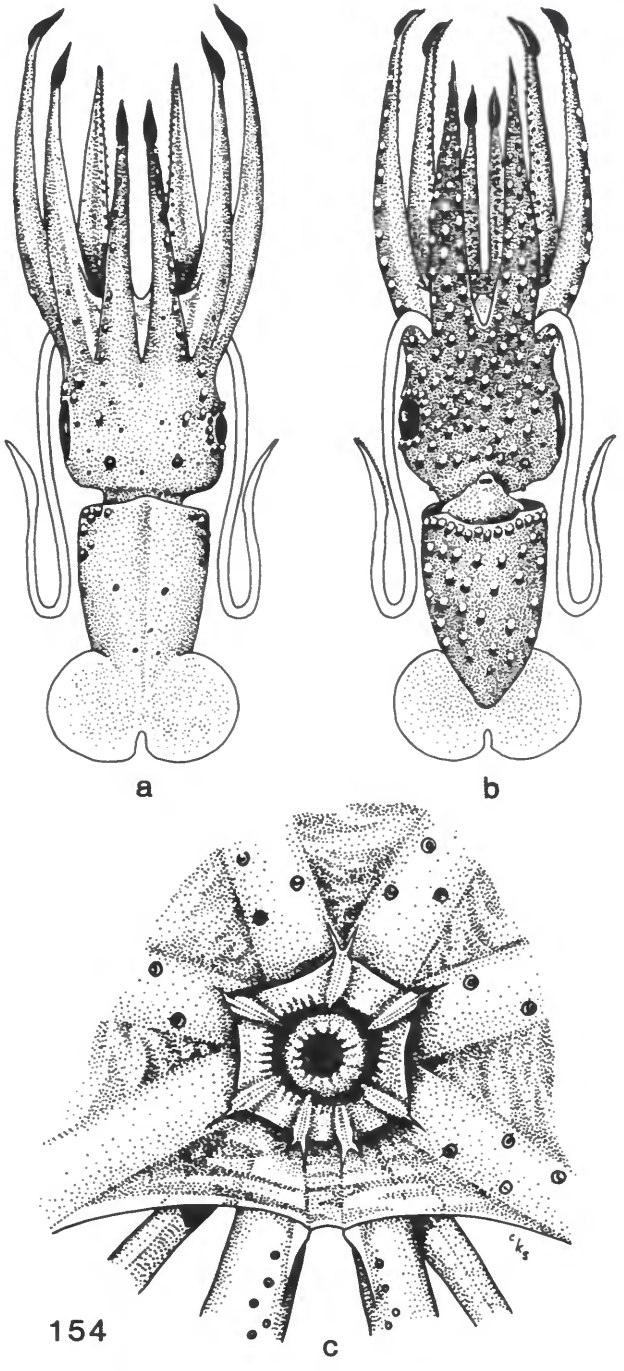

FIGURE 154.—*Histioteuthis macrohista* (*a,b*, 11 mm ML, 40°S, 160°E; *c*, 14 mm ML, 30°S, 13°E): *a*, dorsal view; *b*, ventral view; *c*, buccal view with 7-membered buccal membrane. (From N. Voss, 1969.)

membered buccal membrane; 17 large photophores (may be 16 in one taxon) around right eye; 2–4 conspicuous, large, round photophores may or may not be present on left posteroventral margin of head.

Eggs: Eggs (? oviducal) measured 2.3 mm diameter from mature female (330 mm ML) from off western Greenland; estimated to number ~25,000.

GEOGRAPHICAL DISTRIBUTION.—North Atlantic Subarctic and Temperate regions, including East and West Mediterranean; eastern Atlantic in Mauritanean Upwelling and Tropical Region, extending around South Africa into Indian Ocean to ~30°S in area of Agulhas Current.

VERTICAL DISTRIBUTION.—Closing nets captured a juvenile (9 mm ML) at 305–400 m during the day, and a 31 mm ML juvenile at 240–265 m at night. At night, open nets captured juveniles <10 mm ML at maximum depths of 70–200 m, and juveniles of 10–20 mm ML fishing maximum depths of 100–200 m. Larger juveniles and subadults have been taken at night in eastern Atlantic largely between ~200 m and 800 m. With the exception of one mature female taken off western Greenland at 325 m, mature animals all have been captured below 600 m, with the large majority taken in nets fished below 1000 m to maximum fishing depths of 2200 m.

REMARKS.—Composed of more than one species or subspecies. It is important in the diet of sperm whales in North Atlantic Ocean (Clarke, 1962, 1974).

REFERENCES.—Clarke (1962, 1974), N. Voss (1969, unpublished data), Lu and Clarke (1975b), Kristensen (1980).

Histioteuthis bonnellii corpuscula Clarke, 1980

SPECIES CHARACTERS.—*Young:* Inner web between arms I–III deep; single, enlarged, elongate, terminal photophore on arms I–III; 6-membered buccal membrane; 17 large photophores around right eye; 2–3 conspicuously large, round photophores on left posterior margin of ventral surface of head.

GEOGRAPHICAL DISTRIBUTION.—Known definitely only from original material from stomachs of sperm whales taken at 31°S, 33°W and off South Africa in areas of Benguela and Agulhas currents; Tasman Sea and north of New Zealand.

REMARKS.—This is a poorly known subspecies that matures at small size (~45–83 mm ML). At present, subspecies cannot be clearly separated from one of the undescribed members of the *H. b. bonnellii* group. Additional study may show the two taxa to be identical; if so, the geographic range of *H. b. corpuscula* would extend into more northern waters in the Atlantic. Future analysis of the *bonnellii* complex will probably result in the elevation of *H. b. corpuscula* to the species level.

REFERENCES.—Clarke (1980), Clarke and MacLeod (1982), N. Voss (1969, unpublished data).

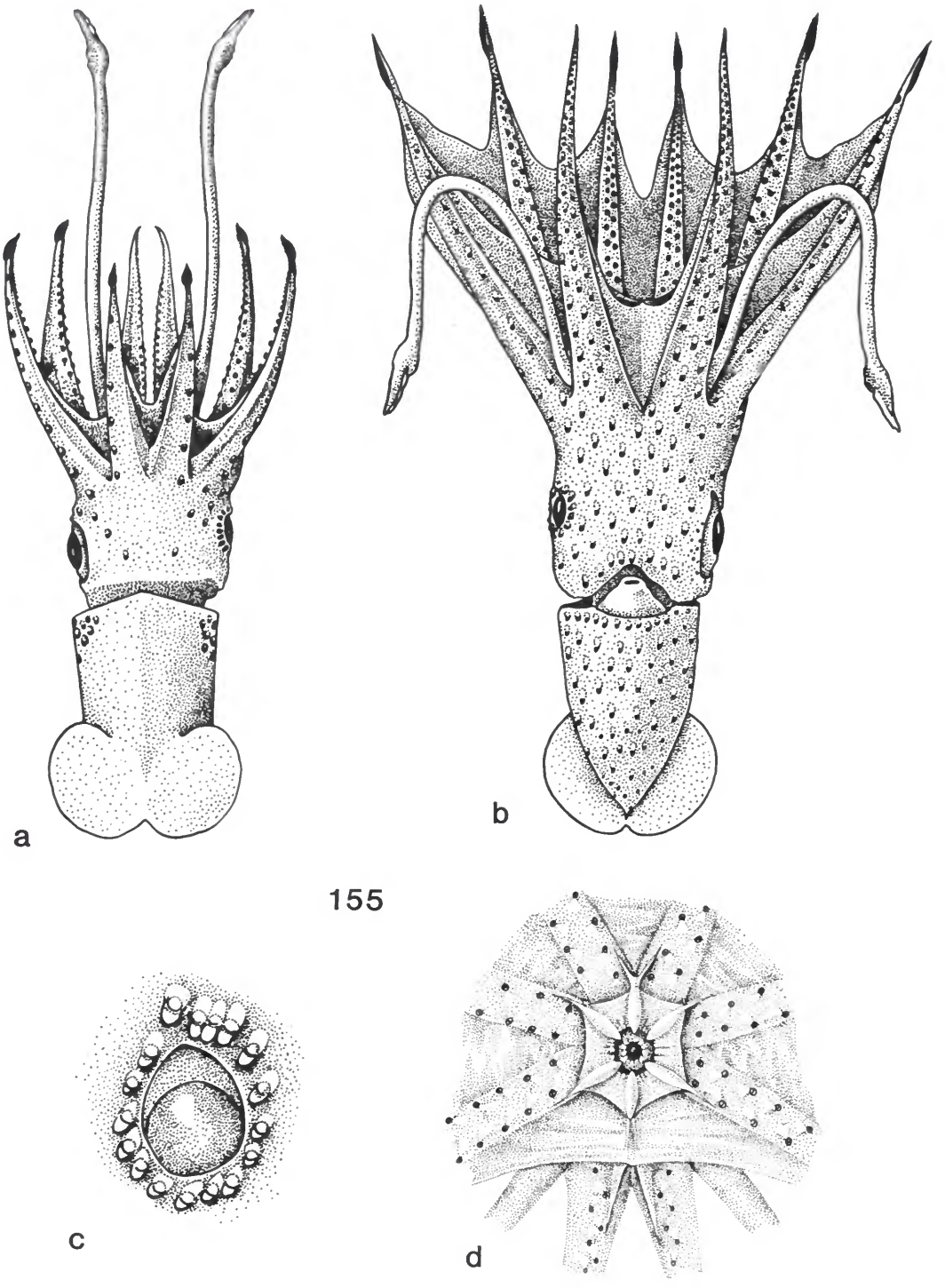

FIGURE 155.—*Histioteuthis bonnellii bonnellii*, eastern North Atlantic temperate specimens (*a*, 9 mm ML, 38°N, 27°W; *b–d*, 21 mm ML, 43°N, 24°W): *a*, dorsal view; *b* ventral view; *c* right eye; *d*, buccal view with 6-membered buccal membrane. (From N. Voss, 1969.)

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Family BATHYTEUTHIDAE Pfeffer, 1900

(by C.F.E. Roper and M.J. Sweeney)

FAMILY CHARACTERS.—*Adults:* Straight funnel locking-cartilage; buccal connectives attach to dorsal borders of arms IV; buccal lappets with minute suckers; suckers on arms in irregular rows (2 rows proximally increasing to 4 distally); many rows of minute suckers on short unexpanded tentacular clubs; fins subterminal, round, or paddle-like; single photophore imbedded at base of arms I–III; entire animal a deep maroon color.

Young: Similar to adults; photophores at base of arms I–III readily apparent in "larvae" (>5 mm ML).

REMARKS.—Monogeneric family.

Bathyteuthis Hoyle, 1885

GENERIC CHARACTERS.—Family is monotypic; generic characters are as given for family.

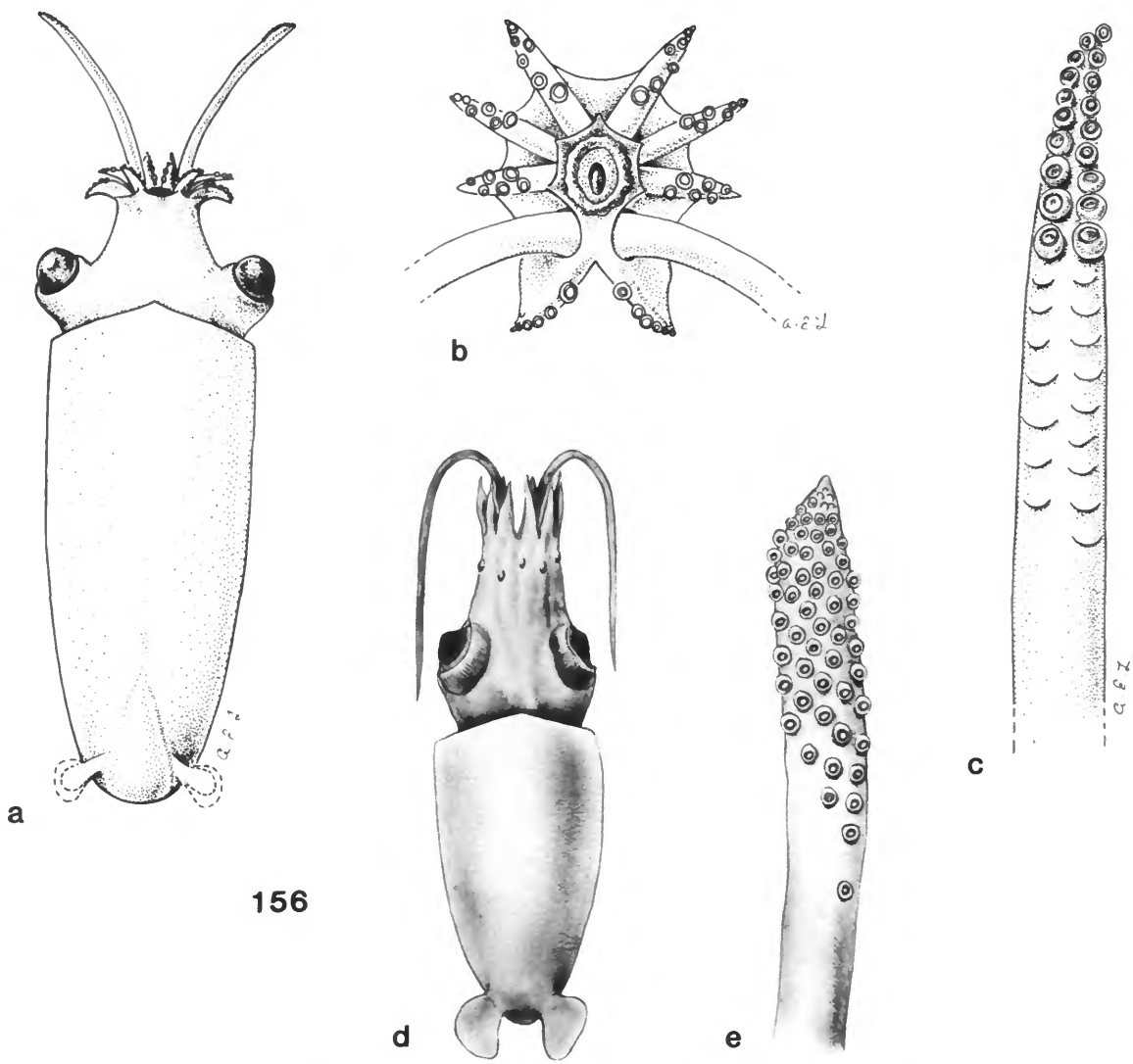

FIGURE 156.—*Bathyteuthis abyssicola* (*a–c*, 4 mm ML, western North Atlantic temperate; *d,e*, 6 mm ML, Antarctic Ocean): *a*, dorsal view; *b*, oral view; *c*, tentacular club (*a–c*, original drawings); *d*, dorsal view; *e*, tentacular club (*d,e*, from Roper, 1969).

Key to Species of Bathyteuthis (Adults and Juveniles)

1. Protective membranes on arms low to well developed, fleshy, with straight to gently scalloped borders; trabeculae not free, enlarged, or elongate 2
   Protective membranes reduced or absent; trabeculae free, elongate, finger-like; arm suckers numerous; sucker rings with 18–34 protuberances; gills long, broad . . . . . ***B. bacidifera***
2. Arm suckers relatively few; sucker rings with 8–18 protuberances; arms short, blunt; gills short, narrow . . . . . ***B. abyssicola***
   Arm suckers extremely numerous; sucker rings with 10–14 protuberances; arms long, attenuate; gills long, broad . . . . . ***B. berryi***

Bathyteuthis abyssicola Hoyle, 1885

SPECIES CHARACTERS.—*Adults* and *Juveniles* (Figure 156): Protective membranes on arms low, fleshy; without free trabeculae; tentacles and clubs relatively short; arm suckers relatively few; sucker rings with 8–18 teeth; gills short, narrow.

GEOGRAPHICAL DISTRIBUTION.—Circumpolar in the Southern Ocean and in highly productive waters of the eastern Pacific, Atlantic, and Indian Oceans.

VERTICAL DISTRIBUTION.—Oceanic species that occurs between about 100 and 4200 m. Normally is encountered between 700 and 2000 m in the Southern Ocean where it carries out a deep diel vertical migration. "Larvae" and juveniles tend to live at shallower depths than the adults (Roper, 1969). Clarke and Lu (1975) and Lu and Clarke (1975) reported diel vertical migration of the population in the eastern tropical-subtropical North Atlantic with the species concentrated between 100 and 1000 m.

Bathyteuthis berryi Roper, 1968

SPECIES CHARACTERS.—*Adults* and *Juveniles:* Protective membranes on arms well developed and fleshy proximally; without free trabeculae; suckers on arms extremely numerous; sucker rings with 10–14 teeth; gills long, broad.

GEOGRAPHICAL DISTRIBUTION.—Eastern Pacific waters off southern California.

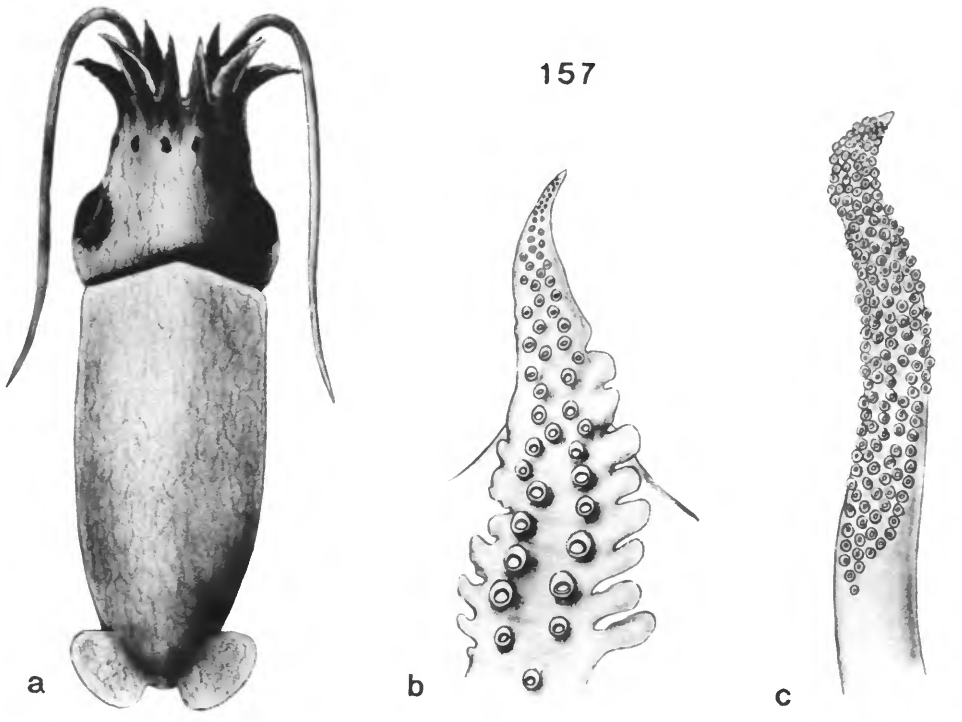

FIGURE 157.—*Bathyteuthis bacidifera*, eastern Pacific temperate: *a*, dorsal view, 11.5 mm ML; *b*, left arm I, 11.5 mm ML; *c*, tentacular club, 17 mm ML. (From Roper, 1969.)

Bathyteuthis bacidifera Roper, 1968

SPECIES CHARACTERS.—*Adults* and *Juveniles* (Figure 157): Protective membranes on arms modified, reduced, but with long, free, finger-like trabeculae present; tentacles and clubs relatively long; suckers on arms numerous; sucker rings with 18–34 teeth; gills long, broad.

GEOGRAPHICAL DISTRIBUTION.—Productive waters of Eastern Pacific Equatorial Water Mass and Indian Ocean Equatorial Water Mass.

REMARKS.—New evidence from recent comparative morphological studies indicates the presence of a possible fourth species in the Caribbean Sea (Toll, 1982; Hess, 1987).

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Family PSYCHROTEUTHIDAE Thiele, 1920

(by C.F.E. Roper and M.J. Sweeney)

FAMILY CHARACTERS.—*Adults* (Figures 158, 159): Buccal connectives attach to dorsal borders of arms IV; arms with 2 rows of suckers; tentacular club with 4–7 rows of suckers on manus and dactylus; straight, simple funnel locking-cartilage; no photophores on mantle or head. Monotypic (see Remarks).

Psychroteuthis Thiele, 1920

GENERIC CHARACTERS.—Family is monotypic; generic characters are as given for family.

Psychroteuthis glacialis Thiele, 1920

SPECIES CHARACTERS.—*Young:* Not described but likely to have all characters given above; body and fin shape probably differs from adult.

GEOGRAPHICAL DISTRIBUTION.—Antarctic and Subantarctic sectors of Atlantic; widespread in Southern Ocean.

VERTICAL DISTRIBUTION.—Reported from depths of slightly less than 200 m to as deep as 700 m in Antarctic and Subantarctic waters.

REMARKS.—Important in the diet of Emperor and Adelie penguins (Offredo et al., 1985). A second undescribed species also from the Antarctic exists.

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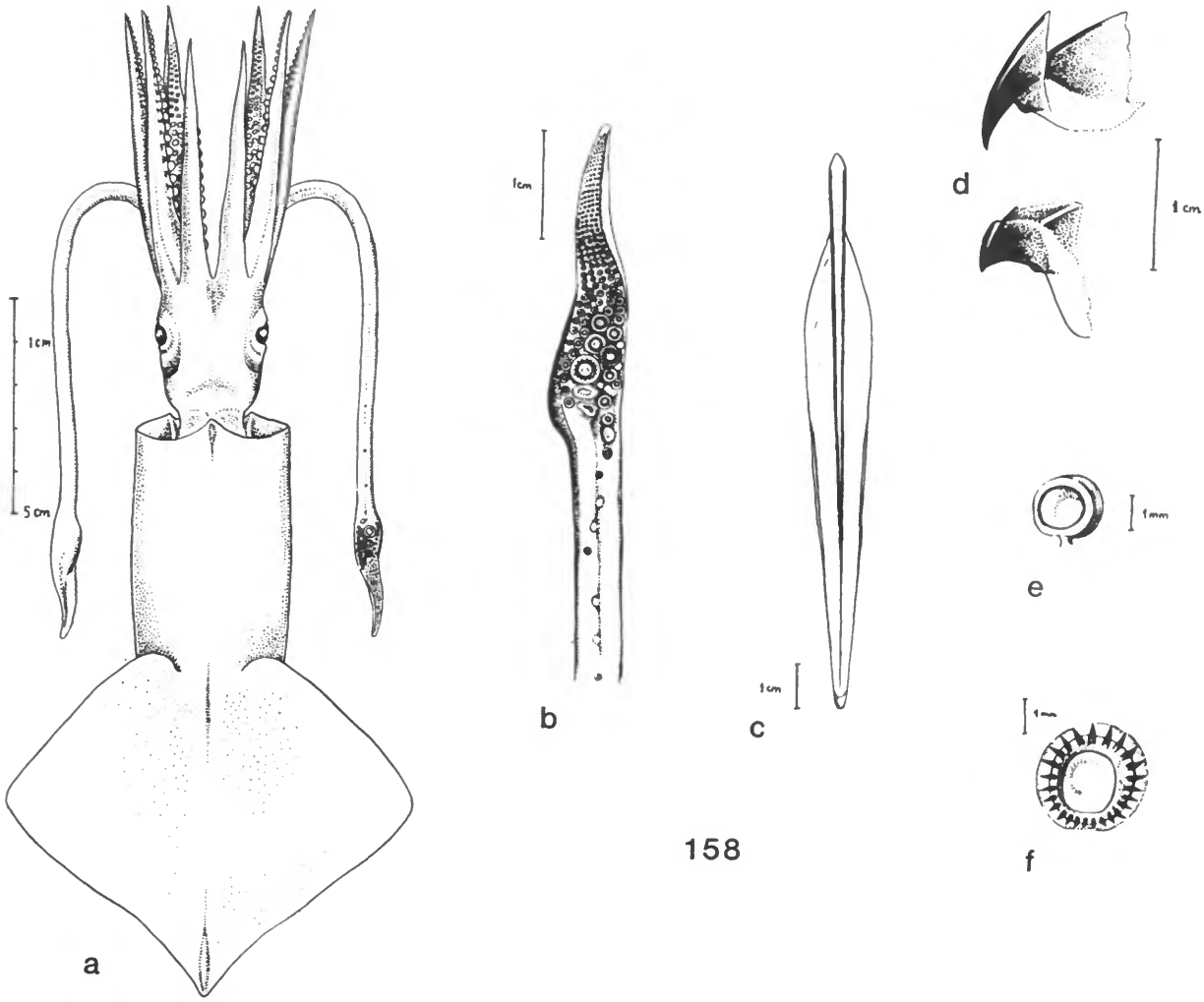

FIGURE 158.—*Psychroteuthis glacialis*, 128 mm ML adult, Antarctic Ocean: *a*, dorsal view; *b*, tentacular club; *c*, gladius; *d*, beaks; *e*, arm sucker; *f*, large tentacular club sucker. (From Filippova, 1972.)

FIGURE 159.—*Psychroteuthis* sp., 167 mm ML adult, Antarctic Ocean, 78°S, 167°E, USNM 730193: *a*, ventral view; *b*, tentacular club; *c*, dorsal view. (Original drawings.)

Family ARCHITEUTHIDAE Pfeffer, 1900

(by C.F.E. Roper)

FAMILY CHARACTERS.—*Adults:* Single genus is characterized by 4 rows of suckers on manus of club with distinct proximal cluster of numerous, small suckers; 2 longitudinal rows of alternating suckers and pads on tentacular stalk; funnel locking-cartilage straight, simple; buccal connectives attach to dorsal border of arms IV; arms long to very long; animals attain very large size, to 3-4 m ML.

Architeuthis Steenstrup, 1860

GENERIC CHARACTERS.—*Young* (Diagnoses from specimens of 45 and 57 mm ML, the smallest currently described; Roper and Young, 1972) (Figure 160): Mantle long, slender, muscular with distinct marginal lobes; fins terminal, small (30%-35% ML), longer than wide (25% ML), rounded and continuous posteriorly; fin insertions broad anteriorly; head circular in cross section, slightly wider than mantle width; eyes large, prominent; funnel locking-cartilage simple, straight, long, narrowest anteriorly; silvery white fibrous tissue covers mantle, head, aboral surface of arms, but is absent from posterior margin of head; nuchal crest distinct but unelevated; arms long (40%-60% ML) to very long (100% ML); arm formula 4 = 3 = 2 >1; protective membranes low, weak on all arms; tentacular clubs long; expanded manus with 4 rows of suckers; suckers of median 2 rows greatly enlarged; 65-100 minute, closely packed suckers irregularly clustered proximal to manus; suckers and knobs on tentacular stalk begin near proximal base of tentacle and become more closely spaced distally; dactylus narrow, elongate, suckers in 4 rows, becoming minute distally.

Note: Recently a larval specimen (Figure 161) of *Architeuthis* (10.3 mm ML) has been reported (Lu, 1986) from the Tasman Sea at 33°19.4′S, 155°00.3′E from 20 m depth. A detailed description is planned (C.C. Lu, pers. comm.).

GEOGRAPHICAL DISTRIBUTION.—In addition to the above specimen, only 3 small specimens have been reported in the literature and these were taken at diverse localities: off Madeira, the Straits of Florida, and off Chile. The family is distributed worldwide with most abundant records from the North Atlantic (Newfoundland, Norway), southwestern Pacific (New Zealand), northwestern Pacific (Japan) and the Southern Ocean (Clarke, 1966; Roper and Boss, 1982).

VERTICAL DISTRIBUTION.—The 3 small specimens of *Architeuthis* were all from stomach contents of predators (Roper and Young, 1975). Roper and Young (1972) described the first two juvenile specimens (45 and 57 mm ML) from 2 *Alepisaurus* sp. stomachs. Depth of consumption was estimated to be in the upper few hundred meters. The third, a larger specimen (167 mm ML) was reported from a *Xiphias gladius* with no estimated depth of consumption given (Toll and Hess, 1981).

REMARKS.—Twenty nominal species have been described, many of them synonyms due to descriptions of incomplete animals. No thorough analysis of extant type material has been done to date to verify and define the species. The specimen recorded by Toll and Hess (1981) was a mature male (167 mm ML) with spermatophores. This is a remarkably small specimen to be mature, given the gigantic size of most of the specimens recorded. Toll and Hess (1981) suggest it might be a previously undescribed small species. Interestingly, specimens from Japanese waters tend to be smaller than those recorded elsewhere.

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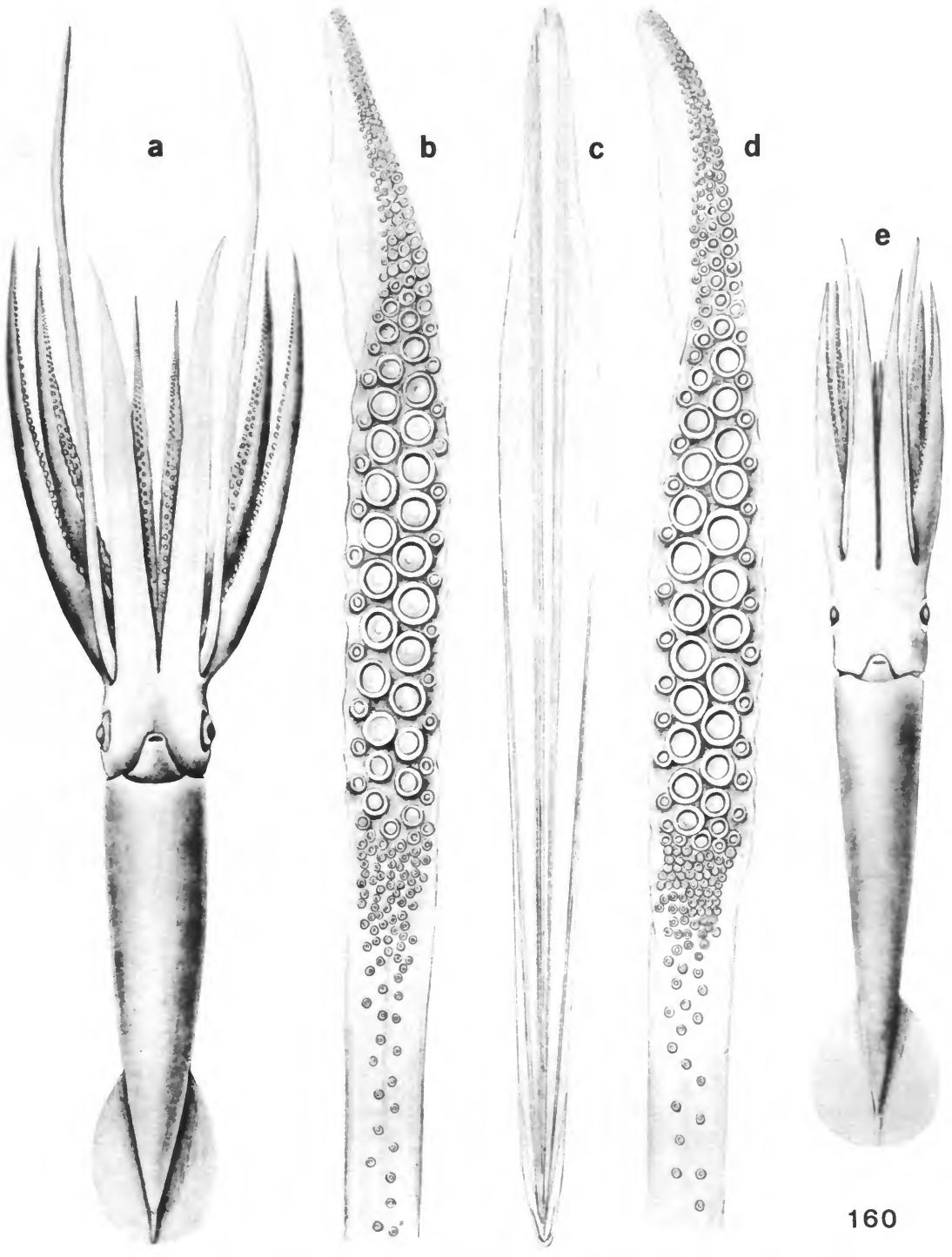

FIGURE 160.—*Architeuthis* sp. (*a–c*, 57 mm ML juvenile, eastern Atlantic; *d,e*, 45 mm ML juvenile, eastern Pacific): *a*, ventral view; *b*, left tentacular club; *c*, gladius; *d*, left tentacular club; *e*, ventral view. (From Roper and Young, 1972.)

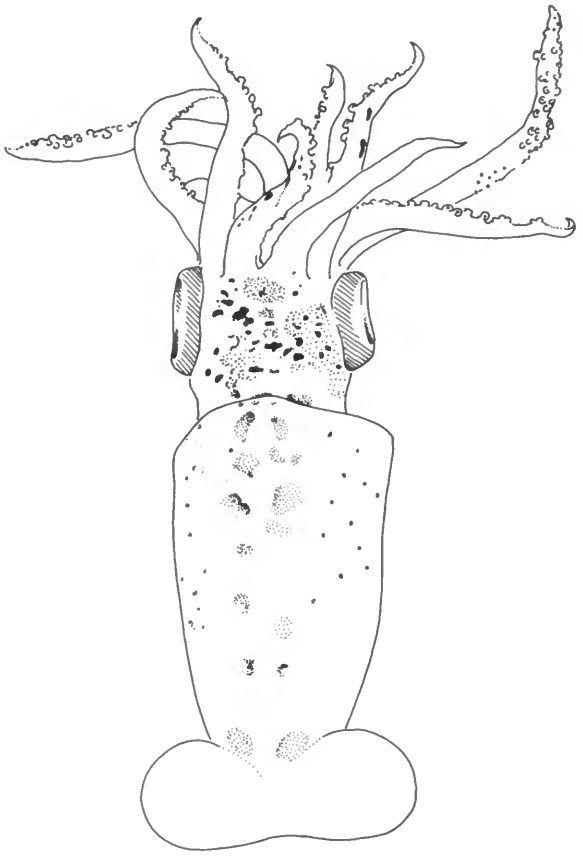

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FIGURE 161.—*Architeuthis* sp., dorsal view, 10 mm ML larva, Tasman Sea. (From Lu, 1986.)

Family NEOTEUTHIDAE Naef, 1921

(by C.F.E. Roper)

FAMILY CHARACTERS.—*Adults* (Figure 162*a,e*): Suckers in 2 rows on arms; tentacular club suckers in 4 rows on distal part of manus and dactylus and numerous small to minute closely packed suckers on proximal part of manus; buccal connectives attach to dorsal borders of arms IV; straight, simple funnel locking-cartilage; anterior fin lobes absent and posterior fin lobes free; photophores absent.

Young (Figure 162*c,d*): Larvae have not been described. Characters for juveniles as for adults; tentacles very small, clubs with numerous minute suckers and buds on proximal part of manus; fins lateral-terminal, broadly separated in dorsal midline.

REMARKS.—Three genera are known, *Neoteuthis* Naef, 1921, *Alluroteuthis* Odhner, 1923, and *Nototeuthis* Nesis and Nikitina, 1986, but the systematics currently is in a very poor state (Roper et al., 1969; Young, 1972). The family designation is Neoteuthidae Naef, 1921:48, rather than Alluroteuthidae Odhner, 1923 (Voss, 1977:576).

Key to Genera* of NEOTEUTHIDAE (Adults and Juveniles)

Fins long, usually >60% ML, and narrow, especially anteriorly; posterior lobes not pronounced; manus of club long, covered with numerous minute suckers that extend proximally along tentacle stalk; distal part of manus with 4 rows of nearly subequal suckers . . . . . ***Neoteuthis***

Fins short, <50% ML, moderately broad, widest in posterior half; posterior lobes prominent, extend posterior to tip of mantle; proximal portion of club (manus) relatively short, with minute suckers; carpal knobs and suckers only extend proximally along tentacular stalk; distal part of manus with 4 rows of suckers, with suckers of median 2 rows greatly enlarged . . . . . ***Alluroteuthis***

**Nototeuthis* is poorly known; genus described from only one juvenile specimen; larvae unknown.

Neoteuthis Naef, 1921

SPECIES CHARACTERS.—Current recognized species of *Neoteuthis* are *Neoteuthis thielei* Naef, 1921; *Neoteuthis* sp. Young (1972); *Neoteuthis* sp. Clarke and Lu (1974, 1975); *Neoteuthis* sp. Okutani (1974).

GEOGRAPHICAL DISTRIBUTION.—Species have been captured in Antarctic waters (*N. thielei*), eastern Pacific (Young, 1972; Okutani, 1974) and eastern Atlantic (Clarke and Lu, 1974, 1975).

VERTICAL DISTRIBUTION.—Smaller specimens are caught in the upper 200–300 m, whereas adults appear to inhabit the deep sea.

REMARKS.—The broadly spaced localities of capture and small number of specimens available have made species definitions extremely difficult. More than one species seems a possibility, but such a decision must await detailed analysis.

Alluroteuthis Odhner, 1923

Alluroteuthis antarcticus Odhner, 1923

SPECIES CHARACTERS.—*Adults* and *Young:* See key; monotypic genus.

GEOGRAPHICAL DISTRIBUTION.—Antarctic Ocean, south of 40°S, probably circumpolar.

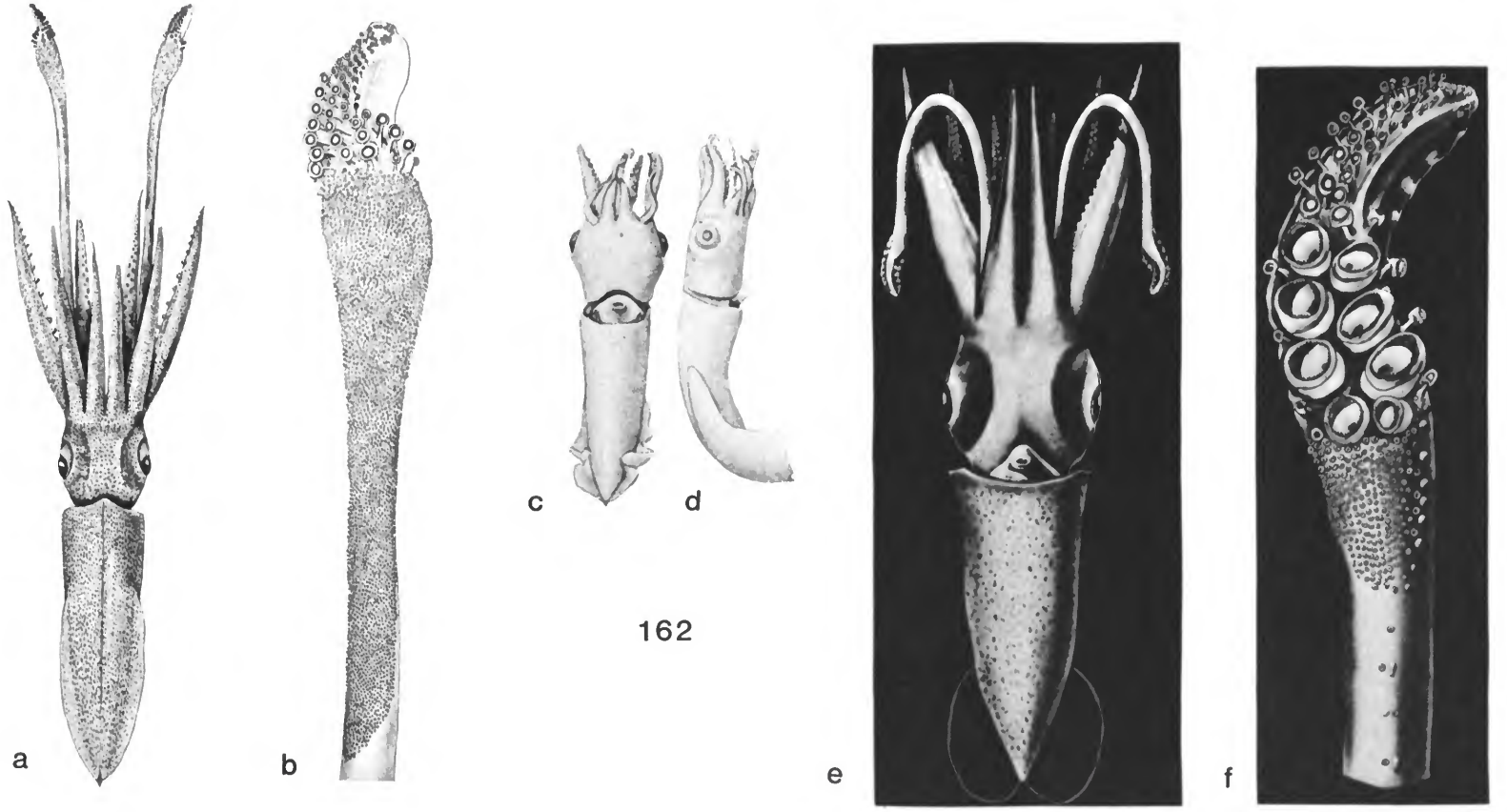

FIGURE 162.—Neoteuthidae (*a,b, Neoteuthis* sp., eastern Pacific, 83 mm ML; *c,d, Neoteuthis? thielei,* South Atlantic, 32°S, 8°W, 11 mm ML larva; *e, f, Alluroteuthis antarctica,* Antarctic Ocean): *a,* dorsal view; *b,* tentacle (*a,b,* from Young, 1972); *c,* ventral view; *d,* lateral view of same (*c,d,* from Thiele, 1920); *e,* ventral view; *f,* tentacle (*e, f,* from Roper, Young, and Voss, 1969).

VERTICAL DISTRIBUTION.—Captures frequent in upper 200 m, but adults, at least, occur deeper.

REMARKS.—*A. antarcticus* has been recorded several times from Antarctic waters since its original description and appears to be quite abundant (Roper, 1969; Nemoto et al., 1985), but little is known about its biology.

Nototeuthis Nesis and Nikitina, 1986

Nototeuthis dimegacotyle Nesis and Nikitina, 1986

SPECIES CHARACTERS.—*Young:* Two greatly enlarged suckers on manus of tentacular club.

GEOGRAPHICAL DISTRIBUTION.—Southeastern Pacific Ocean off southern Chile (50°S, 81°W).

VERTICAL DISTRIBUTION. Single specimen captured in open net that fished 500–0 m.

REMARKS.—The systematic status of this animal is tentative until additional material becomes available for study.

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Family OMMASTREPHIDAE Steenstrup, 1857

(by J.H. Wormuth, R.K. O'Dor, N. Balch, M.C. Dunning, E.C. Forch, R.F. Harman, and T.W. Rowell*)

FAMILY CHARACTERS.—*Adults:* Inverted-T funnel locking-cartilage; lateral funnel adductor; 2 rows of suckers on arms; 4 rows of suckers on tentacular club (except *Illex* with 8 rows on dactylus); photophores in some genera; fusion of funnel and mantle locking-apparatus in some species; characteristic "larval" stage (see below).

Young: Distinctive "larval" form, the "rhynchoteuthion," characterized by fusion of the tentacles into a "proboscis." Proboscis present at hatching (about 1 mm ML), division (separation) of proboscis proceeds as squid grows, proboscis stops growing in length once division begins, tentacles separate between 6 and 10 mm ML; up to inception of division distal tip of proboscis with eight suckers; in some species, two opposing distal suckers larger than others; locking cartilage as in adults. (Figure 163*a–d* illustrates growth series typical of larval development in family.)

Eggs: Only one egg mass observed in nature (Naef, 1923), probably *Illex coindetii* from Mediterranean. Three species spawned in captivity, leading to positive identification of larvae: *Illex illecebrosus* (O'Dor and Balch, 1985), *I. coindetii* (Boletzky et al., 1973), and *Todarodes pacificus* (Hamabe, 1963). *Illex* egg masses may reach 1 m in diameter, probably too delicate to be captured by plankton nets; eggs oval at laying (1 mm long-axis), become spherical as embryos develop. Embryonic development described by Hamabe (1962) and O'Dor et al. (1982). Limited observations indicate ommastrephids lay large, gelatinous egg masses, probably pelagic.

Key to Subfamilies and Genera of OMMASTREPHIDAE (Adults and Juveniles)

(Adapted from Roper et al., 1984)

1. Funnel groove smooth, without foveola or side pockets. Subfamily ILLICINAE 2
   Funnel groove with foveola or with foveola and side pockets 3
2. Dactylus of tentacular club with 8 longitudinal rows of small suckers [Figure 164*a*] . . . . . ***Illex***
   Dactylus of tentacular club with 4 longitudinal rows of small suckers [Figure 164*b*] . . . . . ***Todaropsis***
3. Funnel groove with foveola only, no side pockets [Figure 164*c*]; no light organs. Subfamily TODARODINAE . . 4
   Funnel groove with foveola and generally with side pockets [Figure 164*d*]; light organs present on viscera, mantle, and/or subcutaneous. Subfamily OMMASTREPHINAE 6
4. Both arms IV of males hectocotylized [Figure 164*e*] . . . . . ***Notododarus***
   One arm IV (usually right) of males hectocotylized [Figure 164*f*] 5
5. Protective membranes on arms very low, weakly developed, but trabeculae very strongly developed with pointed cirrus-like projections [Figure 164*g*] . . . . . ***Martialia***
   Protective membranes on arms normally developed with normal, nonprojecting trabeculae [Figure 164*h*] . . . . . ***Todarodes***
6. Two distinct, broken, longitudinal stripes (light organs) on ventral surface of mantle [Figure 165*a*] . . . . . ***Eucleoteuthis***
   No longitudinal stripes on ventral mantle, or if stripes present, not as above 7
7. Funnel and mantle components of locking-apparatus generally fused together [Figure 165*b,d*]; two approximately equal-size, round light organs between ink sac and intestine in juveniles, degenerating in adults; large oval light organ generally evident anteriorly on dorsal mantle . . . . . ***Stenoteuthis***
   Funnel and mantle components of locking-apparatus free, not fused together [Figure 165*c*]; none, one, or two distinctly unequal-size, round light organs between ink sac and intestine in juveniles, degenerating in adults; no large oval light organ evident anteriorly on dorsal mantle 8
8. Tips of arms very attenuate with numerous minute, closely packed suckers [Figure 165*e*] . . . . ***Dosidicus***
   Tips of arms normal, not attenuate [Figure 165*f*]; suckers not unusually numerous, small, or crowded 9
9. Nineteen discrete, round light organs in a distinctive pattern on ventral surface of mantle [Figure 165*g*] . . . . . ***Hyaloteuthis***
   No discrete, round light organs on ventral surface of mantle 10
10. Mantle elongate, slender, posteriorly drawn out into pointed tail [Figure 165*h*]; stripe of luminous tissue (often pinkish) along ventral midline of viscera; side pockets often obscure . . . . . ***Ornithoteuthis***
    Mantle robust, not drawn out posteriorly into tail [Figure 165*f*]: no (pinkish) strip of luminous tissue along ventral midline of viscera; side pockets distinct . . . . . ***Ommastrephes***

REMARKS.—The following species diagnoses of young forms (listed by subfamilies) are tentative; specimens of some species are not sufficiently abundant in present collections to permit precise characterization. A summary of these diagnoses is given in Table 2. Brief diagnoses of adults are adapted from Roper et al. (1984). Researchers should continue to refer to published species lists of adults from a specific geographic area as an indication of occurrence of larval forms. Measurments of proboscis length should be used with caution because of variation in muscular contraction due to effects of preservation.

* Junior authors listed alphabetically.

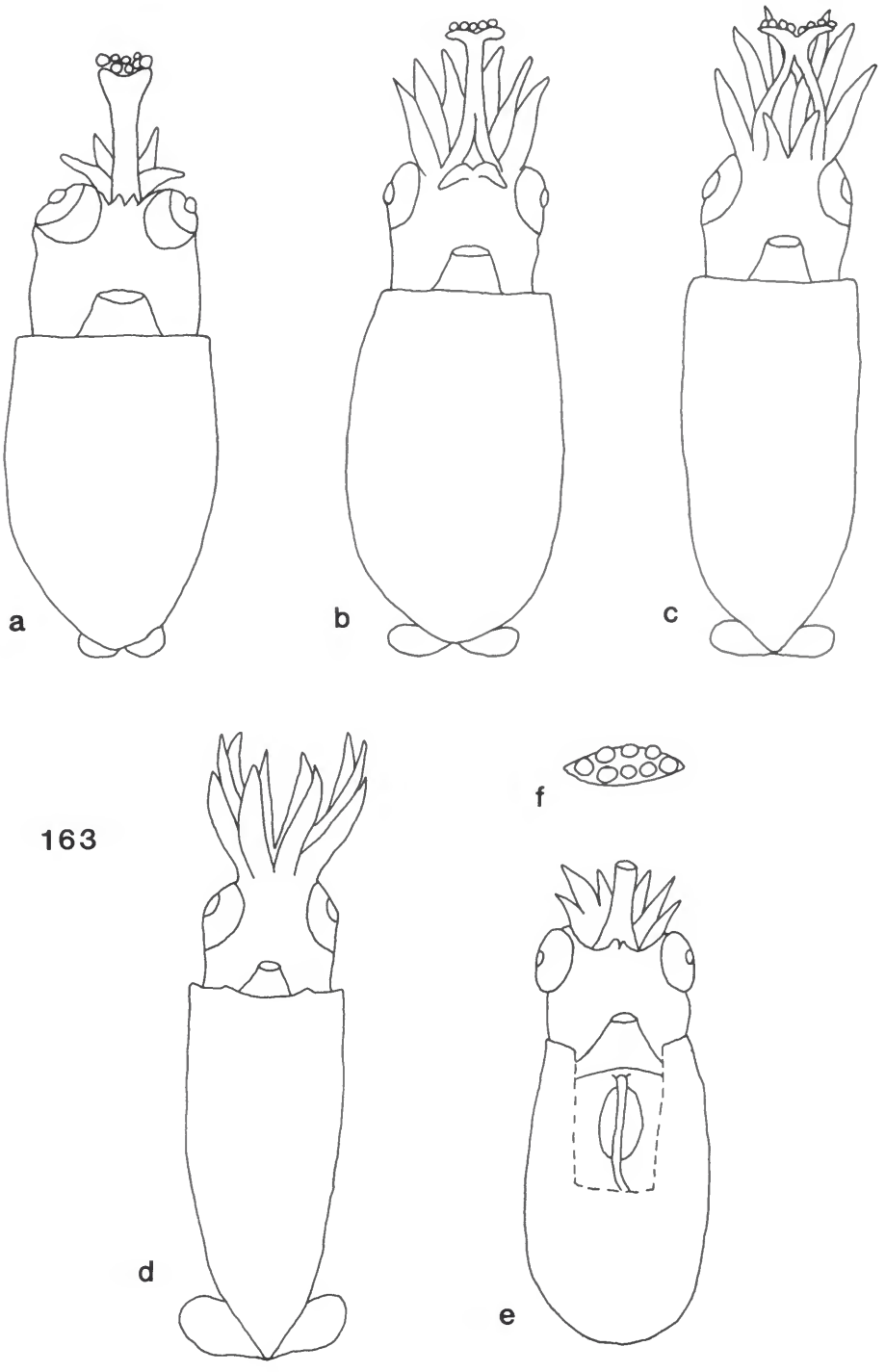


FIGURE 163.—*a–d*, Growth series of typical larvae in the family Ommastrephidae: *a*, 1.5 mm ML; *b*, 4.0 mm ML; *c*, 8.0 mm ML; *d*, 15.0 mm ML. *e, f, Illex* sp., diagrammatic view, western Atlantic: *e*, ventral view with section of mantle removed to show lack of visceral photophore; *f*, end of proboscis with equal-size suckers. (Original drawings.)

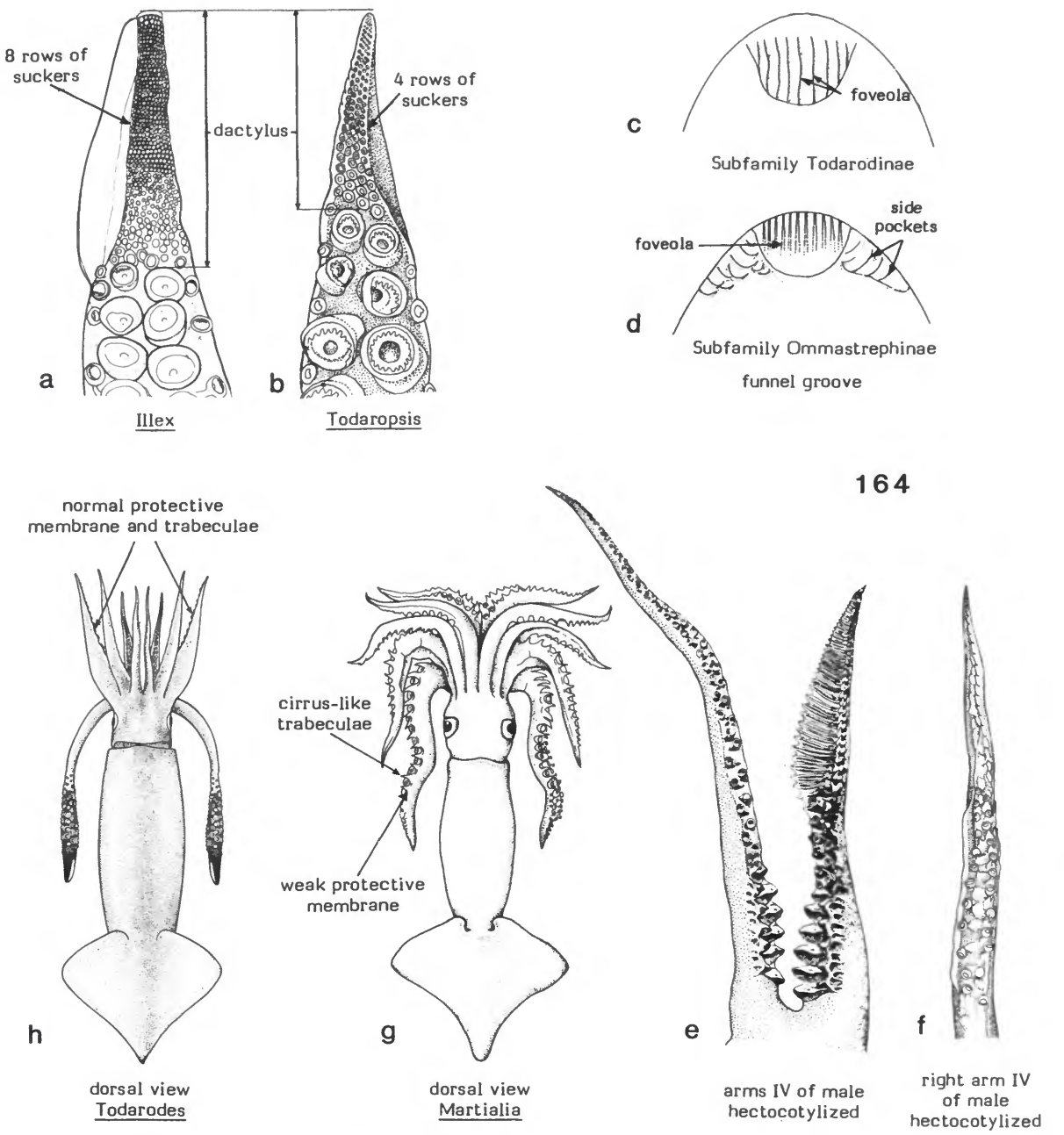


FIGURE 164.—Ommastrephidae: *a*, dactylus of tentacular club with 8 longitudinal rows of suckers (*Illex*); *b*, 4 longitudinal rows of club suckers (*Todaropsis*); *c*, funnel groove with foveola and no side pockets (Todarodinae); *d*, funnel groove with foveola and side pockets (Ommastrephinae); *e*, both arms IV of male hectocotylized; *f*, single (usually right) arm IV hectocotylized; *g*, weakly developed protective membranes and very strongly developed trabeculae; *h*, normally developed protective membranes and trabeculae. (From Roper et al., 1984.)

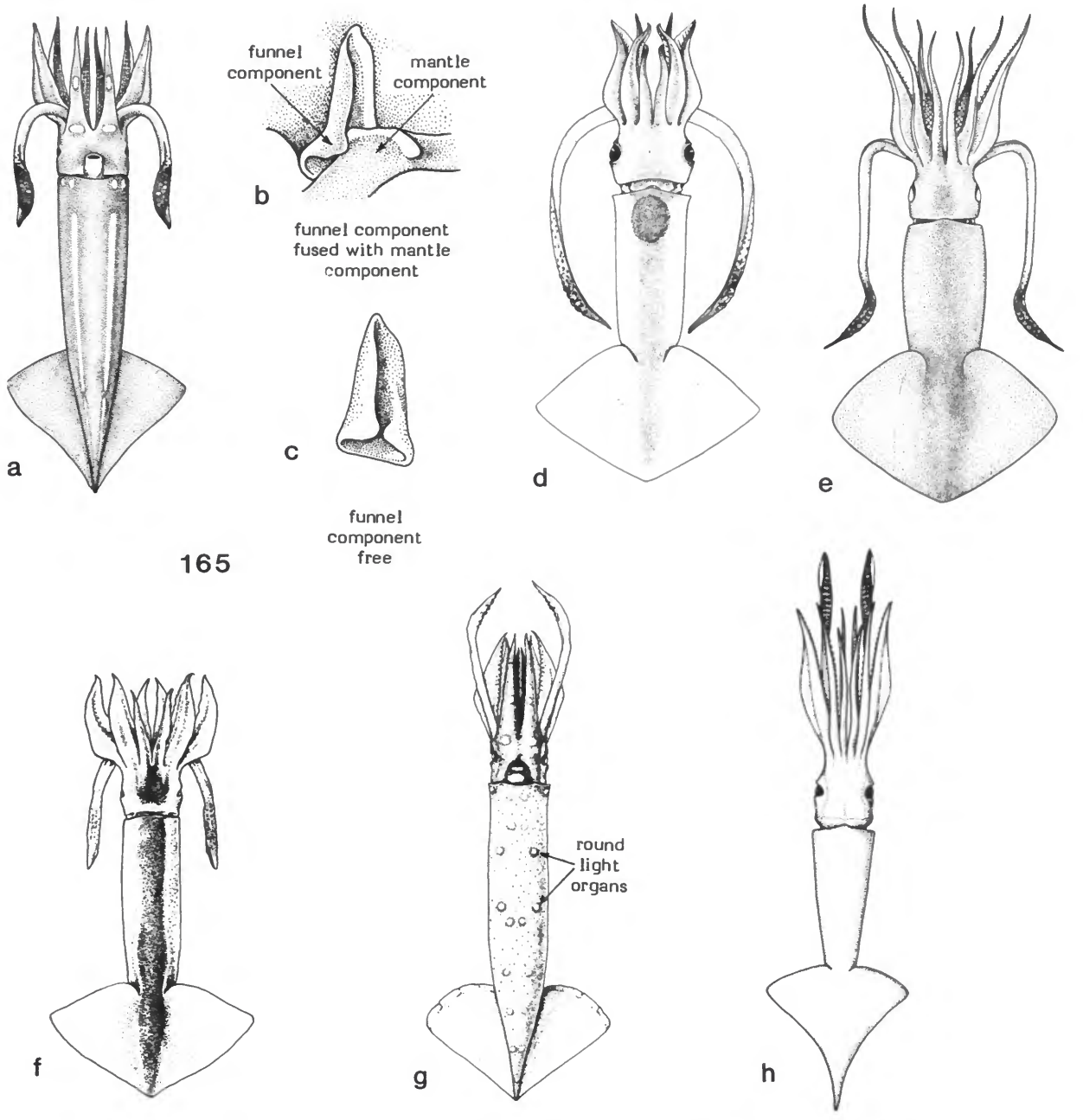


FIGURE 165.—Ommastrephidae: *a*, *Eucleoteuthis*, ventral view; *b*, fused locking-apparatus; *c*, funnel component free from mantle; *d*, *Stenoteuthis*, dorsal view; *e*, arm tips attenuate (*Dosidicus*); *f*, arm tips normal (*Ommastrephes*); *g*, 19 round light organs on ventral mantle (*Hyaloteuthis*); *h*, elongate mantle with pointed tail (*Ornithoteuthis*). (From Roper et al., 1984.)

TABLE 2.—Summary of characters of earliest young stages of ommastrephids. Data are based on workshop studies except for *Dosidicus gigas*, which is from the literature (Nesis, 1983) (=, equal size; ≠, not equal size).

Species*	Photophores		Size (mm ML) at photophore appearance	Lateral proboscis suckers enlarged	Size (mm ML) at proboscis division		Proboscis length as % of ML†	Proboscis length compared to longest arm†
	Ocular	Visceral			Begin	Complete		
PACIFIC								
Stenoteuthis oualaniensis	1	2 (=)	3.5–4.0	No	3.5–4.0	6 (Australia) 9 (Hawaii)	75–100	>>
Ornithoteuthis volatilis	1	2 (≠)	3.5–4.0	Yes	4.0–5.0	6.5–7.0	50–75	
Dosidicus gigas	0	0	-	Yes	5.0–6.0	10	25–50 (80)	>>
Todarodes pacificus	0	0	-	No	N/A	7.9–9.0	25–50	
Nototodarus hawaiiensis	0	0	-	Yes	3.5–4.0	8.0–9.0	25–75	
Nototodarus sloanii/gouldi	0	0	-	No	4.0–4.5	6.0–8.5	25–50	
WORLDWIDE								
Hyaloteuthis pelagica	1	1	<1.5	Yes	3.5–4.0	6.0–6.5	50–75	>
Ommastrephes bartrami	0	0	-	Yes	5.0	7.0	75–100	>>
ATLANTIC								
Illex spp.	0	0	-	No	4.0	10.0	50–75	>>
Stenoteuthis pteropus	1	2 (=)		No	4.5	10.0	50–100	N/A
Ornithoteuthis antillarum	1	2 (≠)		Yes	4.5	6.0	25–50	N/A

* Some species listed in text not included because of insufficient material.
† For specimens of 4.0 mm ML.

The head, arms, and proboscis often are retracted into the mantle, making measurements and identification difficult. Species not described herein are those for which insufficient larval material exists.

Subfamily ILLICINAE Pfeffer, 1912

Illex Steenstrup, 1880

GENERIC CHARACTERS.—*Adults:* Dactylus of tentacular club with 8 rows of small suckers.

Young (Figure 163*e–f*): No ocular or visceral photophores (Figure 163*e*); suckers on proboscis tip nearly equal in size (Figure 163*f*); proboscis length typically 50%–75% ML (<4–8 mm ML); proboscis division begins at about 4 mm ML and tentacles separate by 10 mm ML. Postproboscis young characterized by presence of more than 4 rows of suckers on dactylus and many closely packed suckers and/or sucker buds.

Illex spp. (*I. illecebrosus, I. coindeti, I. oxygonius, I. argentinus*)

SPECIES CHARACTERS.—See Roper et al., 1984, for species descriptions.

GEOGRAPHICAL DISTRIBUTION.—Continental shelf and slope; Atlantic and Mediterranean.

REMARKS.—Youngest forms of *I. illecebrosus* (Lesueur, 1821), *I. coindeti* (Verany, 1837), *I. argentinus* (Castellanos, 1960), and *I. oxygonius* Roper, Lu, and Mangold, 1969, at present cannot be distinguished from each other.

REFERENCES.—Boletzky et al. (1973), O'Dor et al. (1982), O'Dor (1983), Roper and Lu (1978), Rowell and Trites (1985), Vecchione (1978).

Subfamily TODARODINAE Adam, 1960

Todarodes Steenstrup, 1880

GENERIC CHARACTERS.—*Adults:* Right arm IV (rarely left) hectocotilized; funnel groove with foveola, no side pockets; protective membrane normally developed with non-projecting trabeculae; no ocular or visceral photophores.

Young: Young stages of *T. sagittatus* and *T. angolensis* are unkown.

REMARKS.—*T. filippova* is considered a synonym of *T. angolensis* by Nesis (1982).

Todarodes pacificus (Steenstrup, 1880)

SPECIES CHARACTERS.—*Adults:* Fin length 40%–45% ML, sagittate; tentacular club expanded, long; arm sucker rings smooth proximally with 10–14 graded sharp teeth distally.

Young (Figure 166): No ocular or visceral photophores (Figure 166*a*); mantle chromatophore pattern shown in Figure 166*c,d;* probsoscis length typically somewhat longer than longest arms; diameter of suckers on proboscis tip approximately equal size (Figure 166*b*); division of proboscis appears to begin at about 4 mm ML and tentacles are separate at 7–9 mm ML.

GEOGRAPHICAL DISTRIBUTION.—Continental shelf waters of western and northern Pacific from northern Australia to Japan to eastern North Pacific (disjunct distribution?).

REFERENCES.—Dunning (1985), Okutani (1965, 1980).

Nototodarus Pfeffer, 1912

GENERIC CHARACTERS.—*Adults:* Both arms IV of males hectocotylized; funnel groove with foveola only; side pockets and light organs absent.

Young: No ocular or visceral photophores; proboscis length typically 25%–75% ML; diameter of suckers of proboscis tip approximatley equal (*N. sloani/gouldi*) or with two lateral suckers 150%–200% larger than remaining six (*N. hawaiiensis*); division of proboscis begins at 3.5–4.5 mm ML and tentacles separated at 6–9 mm ML.

Nototodarus hawaiiensis (Berry, 1912)

SPECIES CHARACTERS.—*Adults:* Fin length 38%–40% ML; fin angle 50°–57°; tentacular club length 70% of tentacle length; largest club sucker rings with 15–16 large conical pointed teeth, central tooth enlarged; arm sucker rings with 19–21 small conical (distal) to round (proximal) teeth.

Young (Figure 167): No ocular or visceral photophores; mantle chromatophore pattern, when evident, shown in Figure 167; proboscis length typically 25%–75% ML (≥4 mm ML); proboscis length approximately equal to or slightly longer than longest arms; diameter of lateral (distal) suckers on proboscis tip 150%–200% that of remaining six (Figure 167 inserts); division of proboscis begins at about 3.5–4.0 mm ML and tentacles separate at 8–9 mm ML.

GEOGRAPHICAL DISTRIBUTION.—Hawaiian Islands, northern Australia (?Indo-west Pacific).

VERTICAL DISTRIBUTION.—Surface to about 500 m.

REFERENCES.—Dunning (1985), Harman and Young (1985), Wormuth (1976).

Nototodarus sloanii (Gray, 1849) / *gouldi* (McCoy, 1888)

SPECIES CHARACTERS.—*Adults:* Fin length 42%–48% ML, fin angle 40°–55°; tentacular club length 60%–70% of tentacle length.

Young (Figure 168): No ocular or visceral photophore (Figure 168*a*); mantle chromatophores without distinctive

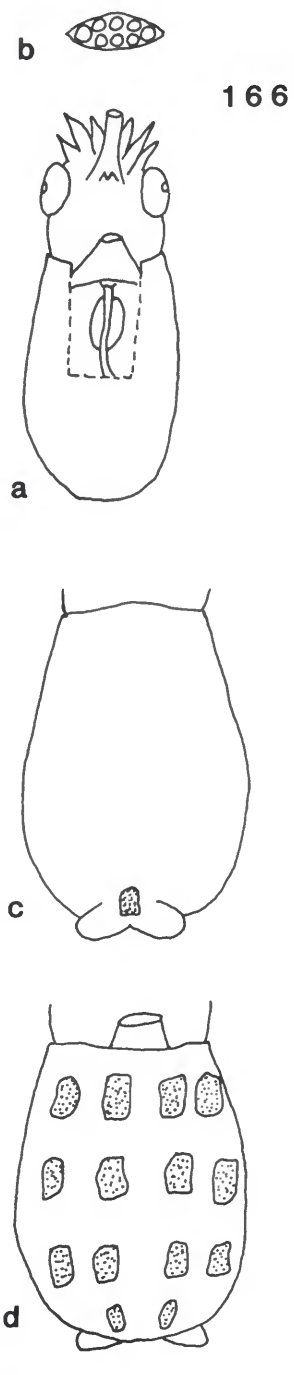


FIGURE 166.—*Todarodes pacificus*, diagrammatic views: *a*, ventral view (section of mantle removed to show lack of visceral photophore); *b*, end of proboscis with equal-size suckers; *c*, dorsal view of mantle with single chromatophore; *d*, ventral view of mantle with chromatophore pattern. (All original drawings.)

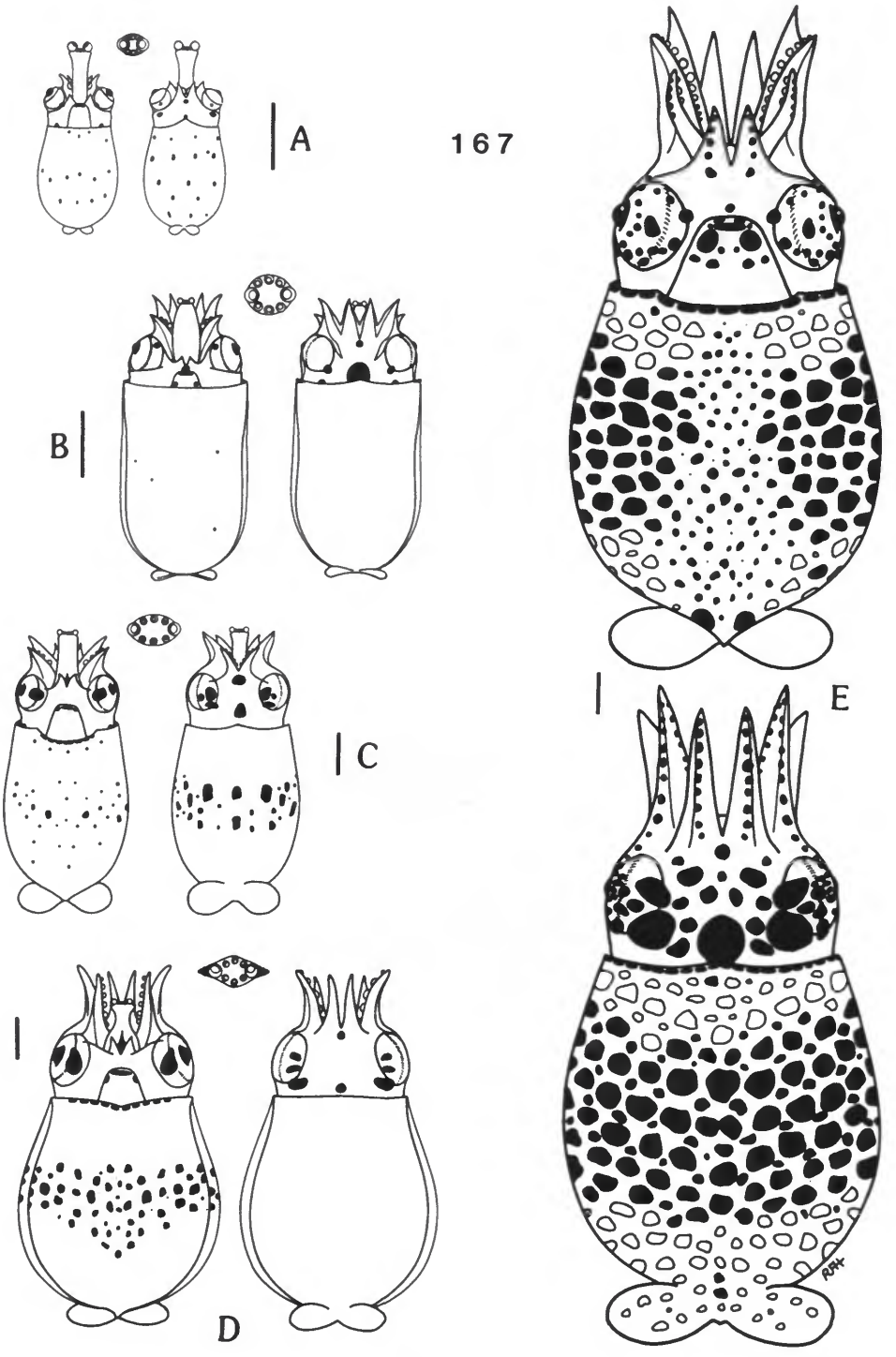


FIGURE 167.—*Nototodarus hawaiiensis*, dorsal and ventral views of larval stages, Hawaiian waters: *a*, 1.7 mm ML; *b*, 3.0 mm ML; *c*, 4.5 mm ML; *d*, 5.8 mm ML; *e*, 9.2 mm ML. Inserts show proboscis tips. Scale bar = 1.0 mm. (From Harman and Young, 1985.)

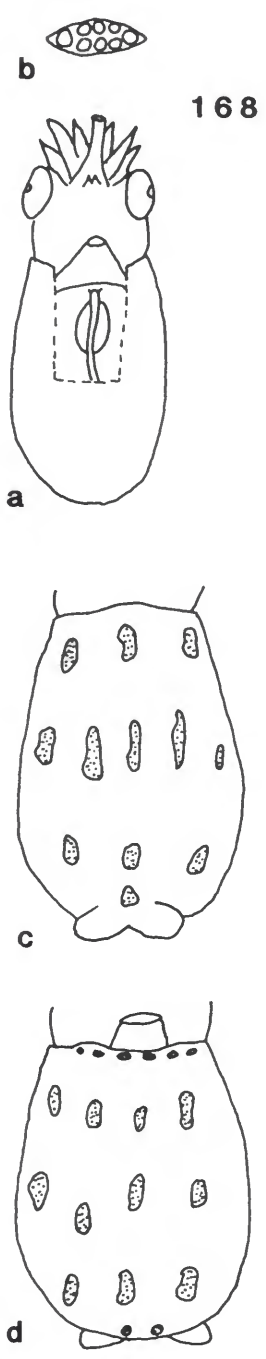


FIGURE 168.—*Nototodarus sloanii / gouldi*, diagrammatic views: *a*, ventral view (section of mantle removed to show lack of visceral photophore); *b*, end of proboscis with equal-size suckers; *c*, dorsal and; *d*, ventral view of mantle with nondistinctive chromatophore pattern. (All original drawings.)

pattern, when evident (<4 mm ML) commonly arranged in 3-4 bands (Figure 168*c,d*); proboscis typically 25%-50% ML; suckers on proboscis tip approximately of equal size (Figure 168*b*); proboscis division begins at about 4.0-4.5 mm ML and tentacles are separate at 6.0-8.5 mm ML.

GEOGRAPHICAL DISTRIBUTION.—*N. gouldi:* Australian waters south of 27°S and around North Island of New Zealand. *N. sloanii:* Around southern New Zealand, Chatham, Auckland, and Campbell Islands.

VERTICAL DISTRIBUTION.—Continental shelf from surface to 500 m.

REMARKS.—At this time "larvae" of these two species are not distinguishable.

REFERENCES.—Mattlin et al. (1985), Okutani and Kuroiwa (1985), Roper et al. (1984), Smith et al. (1981, 1987), Voss (1963).

Subfamily OMMASTREPHINAE Pfeffer, 1912

Ommastrephes d'Orbigny, 1830

GENERIC CHARACTERS.—*Young:* Monotypic genus; see species.

Ommastrephes bartramii (Lesueur, 1821)

SPECIES CHARACTERS.—*Adults:* Fin length 40%-45% ML, width 60% ML, fin angle 45°-50°; long, irridescent (golden or silvery) stripe along ventral midline from mantle opening to level of fin insertion; additional golden patches on head and arms; 4-6 small suckers on tentacular stalk proximal to first smooth knob of carpal fixing apparatus.

Young (Figure 169*a-d*): No ocular or visceral photophores in larvae (Figure 169*a*); chromatophore pattern, when evident, shown in Figure 169*c,d;* length of proboscis typically 75%-100% (<4 mm ML); diameter of lateral (distal) 2 suckers on proboscis tip up to 200% that of remaining 6 suckers (Figure 169*b*); division of proboscis begins at 5 mm ML and tentacles are separate at 7 mm ML.

GEOGRAPHICAL DISTRIBUTION.—Worldwide; subtropical to warm/temperate.

VERTICAL DISTRIBUTION.—Oceanic; surface to 1500 m, mostly upper 200 m.

REFERENCES.—Araya (1983), Dunning and Brandt (1985), Nesis (1979), Okutani (1980), Roeleveld (1982), Wormuth (1976).

Stenoteuthis Verrill, 1880

GENERIC CHARACTERS.—*Young:* With a pair of ocular and 2 equal-size visceral photophores; proboscis typically 50%-

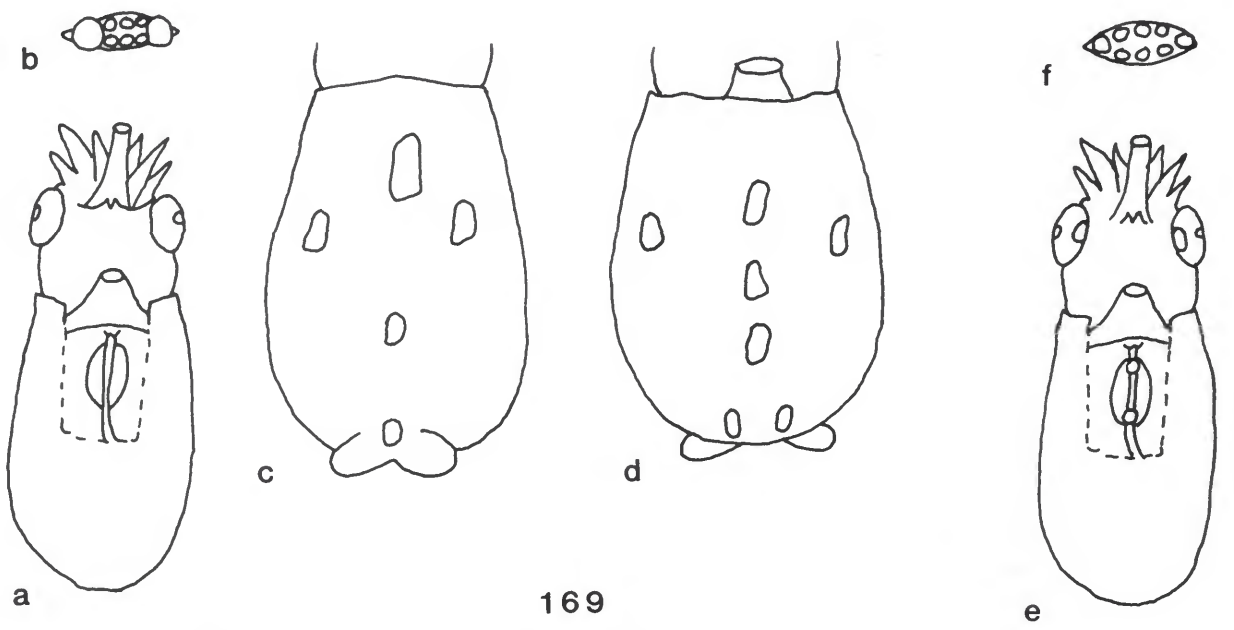


FIGURE 169.—*a–d, Ommastrephes bartramii,* diagrammatic views: *a,* ventral view (section of mantle removed to show lack of visceral photophore); *b,* end of proboscis with greatly enlarged lateral (distal) suckers; *c,* dorsal and; *d,* ventral view of mantle with typical chromatophore pattern. *e,f, Stenoteuthis pteropus,* diagrammatic views: *e,* ventral view (section removed to show presence of visceral photophores, as well as eye photophore); *f,* end of proboscis with equal size suckers. (All original drawings.)

100% ML; diameter of proboscis suckers approximately equal; division of proboscis begins at 3.5–4.5 mm ML, completed by 10 mm ML.

Stenoteuthis pteropus (Steenstrup, 1855)

SPECIES CHARACTERS.—*Adults:* Fins muscular, length 45%–50% ML, width 75%–80% ML, fin angle 55°–60°; large oval subcutaneous patch of of very densely packed, small light organs present on anterodorsal surface of mantle; 0–2 small suckers on tentacular stalk proximal to first smooth knob on carpal fixing apparatus.

Young (Figure 169*e,f*): Identification of young stages tentative because of small collections and of similarities to *Stenoteuthis oualaniensis* from Pacific. Single, round photophore on ventral surface of each eye (Figure 169*e*); 2 equal-size photophores on intestine, 1 anterior, 1 posterior (Figure 169*e*); proboscis length typically 50%–100% ML (<4 mm ML); diameter of suckers on proboscis tip approximately of equal size (Figure 169*f*); division of proboscis begins at about 4.5 mm ML and tentacles are separate at 10 mm ML.

GEOGRAPHICAL DISTRIBUTION.—Atlantic, tropical/subtropical, approximately 40°N to 30°S.

VERTICAL DISTRIBUTION.—Oceanic; surface to about 1500 m, mostly upper 200 m.

REFERENCES.—Nesis (1979), Roeleveld (1982).

Stenoteuthis oualaniensis (Lesson, 1830)

SPECIES CHARACTERS.—*Adults:* Fin length 39%–50% ML, width 69%–86% ML; fin angle 64°(61°–71°); mantle-funnel locking-apparatus fused; a large oval subcutaneous patch of small, closely packed light organs on anterodorsal surface of mantle; 4–5 small suckers on tentacular stalk proximal to first smooth knob of carpal fixing apparatus.

Young (Figure 170): Single, round photophore on ventral surface of each eye (>4 mm ML) (Figure 170*c,d*); 2 equal-size photophores on intestine, one anterior, one posterior (>4 mm ML); mantle chromatophore pattern, when evident, shown in Figure 170*b,c;* proboscis length typically 75%–100% ML (<4 mm ML); proboscis length always much longer than longest arms; diameter of suckers on proboscis tip approximately equal (Figure 170 inserts); division of proboscis begins at about 3.5–4.0 mm ML and tentacles separated at 6 mm ML (Australia) and 9 mm ML (Hawaii).

GEOGRAPHICAL DISTRIBUTION.—Widespread in tropical

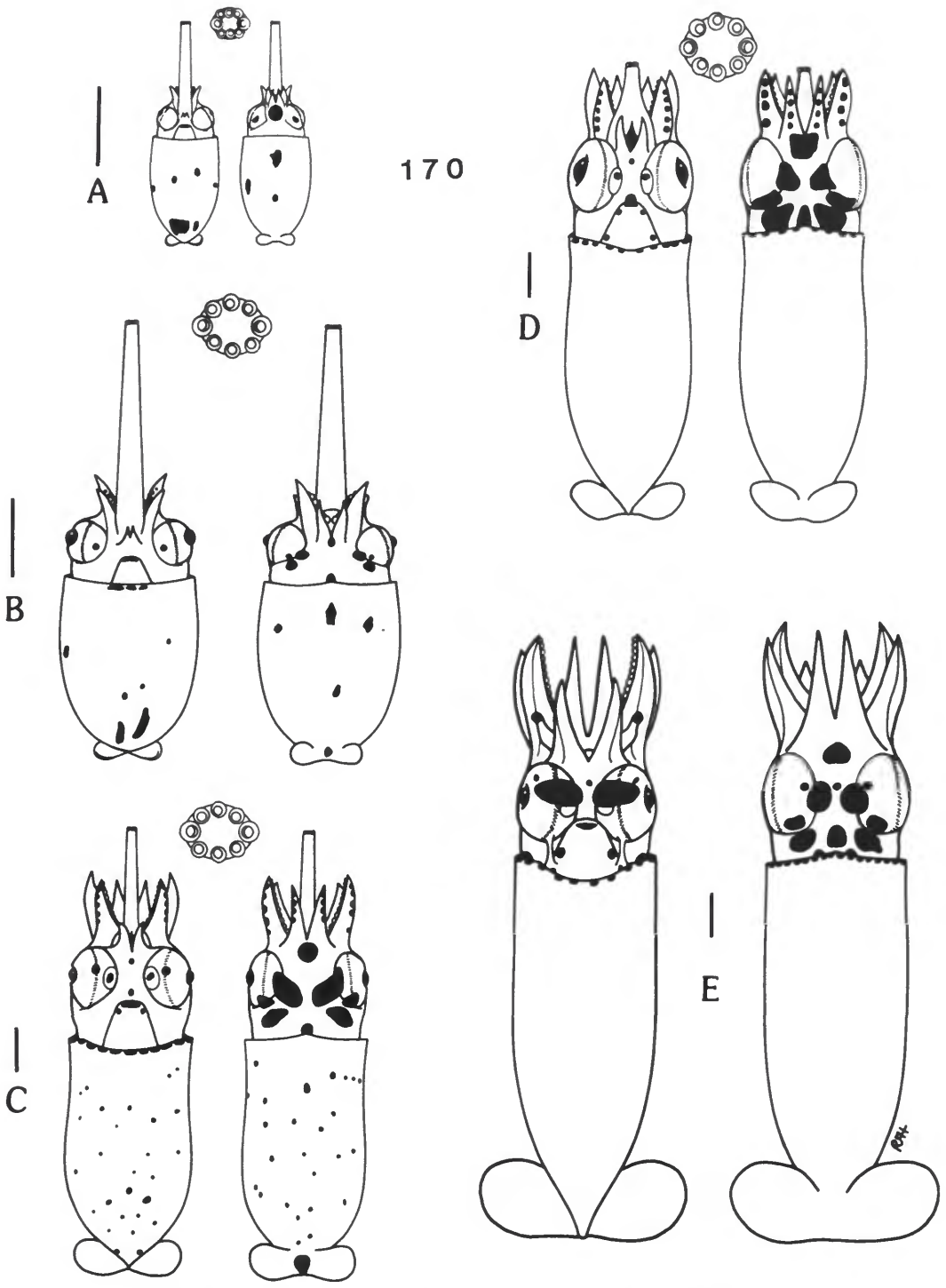


FIGURE 170.—*Stenoteuthis oualaniensis*, dorsal and ventral views of larval stages, Hawaiian waters: *a*, 1.4 mm ML; *b*, 2.3 mm ML; *c*, 5.8 mm ML; *d*, 7.1 mm ML; *e*, 9.1 mm ML. Inserts show proboscis tips. Scale bar = 1.0 mm. (From Harman and Young, 1985.)

and subtropical Pacific and Indian Ocean.

VERTICAL DISTRIBUTION.—Oceanic; surface to perhaps 1000 m, concentrated in upper waters.

REFERENCES.—Dunning and Brandt (1985), Harman and Young (1985), Okutani and Tung (1978), Roeleveld (1982), Wormuth (1976).

Ornithoteuthis Okada, 1927

GENERIC CHARACTERS.—*Adults:* Mantle elongate, slender, posteriorly drawn out into pointed tail; stripe of luminous tissue along ventral midline of viscera (not distinct light organ); side pockets often obscure.

Young: Single, round photophore on ventral surface of each eye; 2 unequal-size photophores on intestine; proboscis length typically 25%-75% ML (<4 mm ML); diameter of lateral (distal) 2 proboscis suckers up to 150% that of remaining 6 suckers; division of proboscis begins at ~4-5 mm ML and tentacles separated at 6-7 mm ML.

Ornithoteuthis antillarum Adam, 1957

SPECIES CHARACTERS.—*Adults:* Mantle narrow, drawn out into long, pointed tail; fins long, sagittate; funnel groove with foveola (7-12 indistinct folds) and side pockets (often obscure); no external light organs, but several on viscera; tentacular club moderately expanded, but no carpal fixing apparatus (no knobs) on stalk.

Young (Figure 171*a,b*): Identification of young tentative because of small collections and of similarities to *O. volatilis* in the Pacific. Single, round photophore on ventral surface of each eye (Figure 171*a*); 2 unequal-size photophores on intestine, anterior one larger, posterior one smaller and develops later (Figure 171*a*); length of proboscis typically 25%-50% ML (<4 mm ML); lateral (distal) 2 suckers on proboscis tip larger than remaining 6 suckers (Figure 171*b*); division of proboscis begins at about 4 mm ML and tentacles separated at 6 mm ML.

GEOGRAPHICAL DISTRIBUTION.—North Atlantic to about 10°S in South Atlantic, tropical/subtropical.

VERTICAL DISTRIBUTION.—Oceanic, surface to 1100 m, mostly 100-600 m.

REFERENCES.—Nesis (1979), Voss (1957).

Ornithoteuthis volatilis (Sasaki, 1915)

SPECIES CHARACTERS.—*Adults:* Mantle very narrow, drawn out into long, pointed tail; fins long, sagittate, sharply

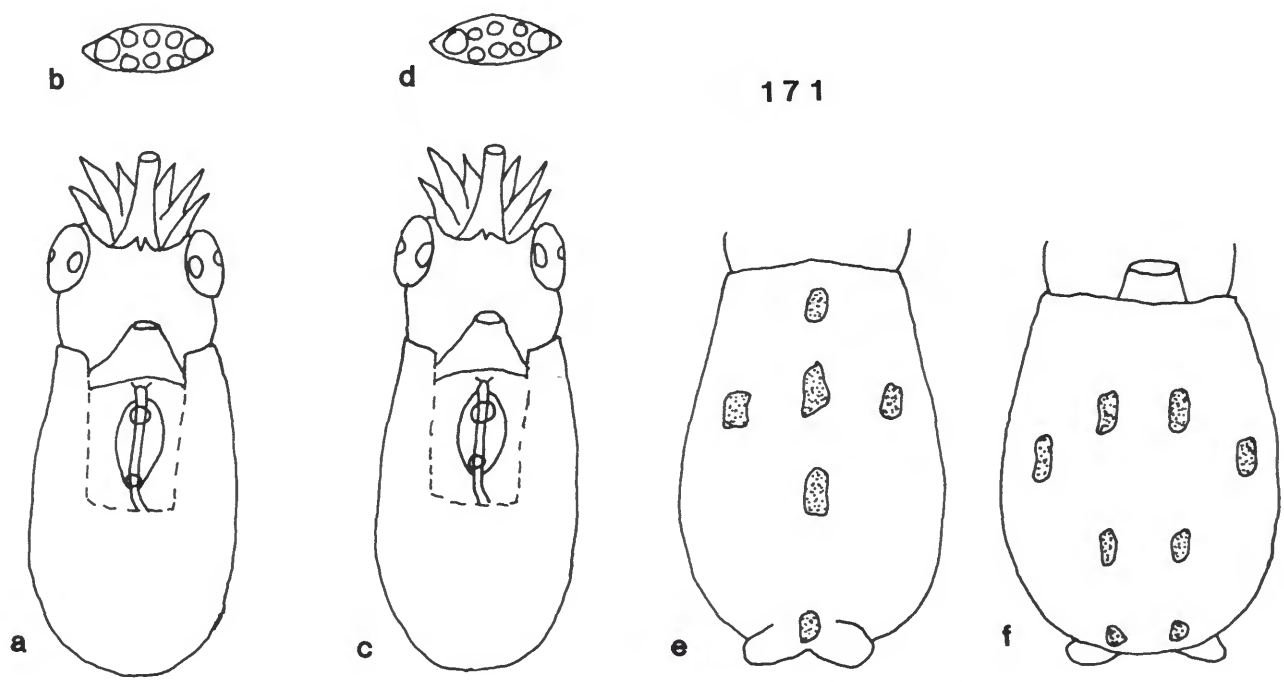


FIGURE 171.—*a,b, Ornithoteuthis antillarum,* diagrammatic views: *a,* ventral view (section of mantle removed to show presence of visceral photophores, as well as eye photophore); *b,* end of proboscis with two enlarged lateral (distal) suckers. *c-f, Ornithoteuthis volatilis,* diagrammatic views: *c,* ventral view (section of mantle removed to show presence of visceral photophores, as well as eye photophore); *d,* end of proboscis with two enlarged lateral (distal) suckers; *e,* dorsal and; *f,* ventral view of mantle with chromatophore pattern. (All original drawings.)

lanceolate posteriorly, length 55% ML, width 47% ML; fin angle 27°; a large oval light organ on intestine; tentacular clubs expanded with very large manal suckers.

Young (Figure 171*c–f*): Single, round photophore on ventral surface of each eye (≥4 mm ML) (Figure 171*c*); 2 unequal-size photophores (smaller, posterior one; larger, anterior one) on intestine (>3.5 mm ML) (Figure 171*c*); mantle chromatophore pattern, when evident, shown in Figure 171*e, f;* proboscis length typically 50%–75% ML (<4 mm ML); proboscis length approximately equal to longest arms; lateral (distal) 2 suckers on proboscis tip up to 150% that of remaining 6 suckers (Figure 171*d*); division of proboscis begins at ~4–5 mm ML and tentacles separated at ~6.5–7.0 mm ML.

GEOGRAPHICAL DISTRIBUTION.—Indo-Pacific, subtropical/warm temperate.

VERTICAL DISTRIBUTION.—Oceanic and slope waters.

REFERENCES.—Dunning and Brandt (1985), Nesis and Nigmatullin (1979), Okutani (1980), Wormuth (1976).

Dosidicus Steenstrup, 1857

GENERIC CHARACTERS.—Monotypic genus; see species.

Dosidicus gigas (Orbigny, 1835)

SPECIES CHARACTERS.—*Adults:* Very large; fins rhomboidal, broad, length 45% ML, fin angle 57°; distal ends of arms drawn out to very long attenuate tips with 100–200 minute, closely packed suckers.

Young (Figure 172): Hatchling about 1 mm ML (Figure 172*a*); no light organs described; dispersed dark brown chromatophores without distinct pattern (Figure 172*e*); length of proboscis typically 25%–50% ML; lateral (distal) 2 suckers on proboscis tip larger than other 6 suckers; arms III and IV distinct at ~1.5–3.0 mm ML and tentacles separated at ~10 mm ML; tentacular fixing apparatus develops only at about 50 mm ML.

GEOGRAPHICAL DISTRIBUTION.—Eastern Pacific, from Tierra del Fuego to Mexico, irregularly cyclical from Mexico to Southern California and Gulf of California.

VERTICAL DISTRIBUTION.—Oceanic and neritic waters.

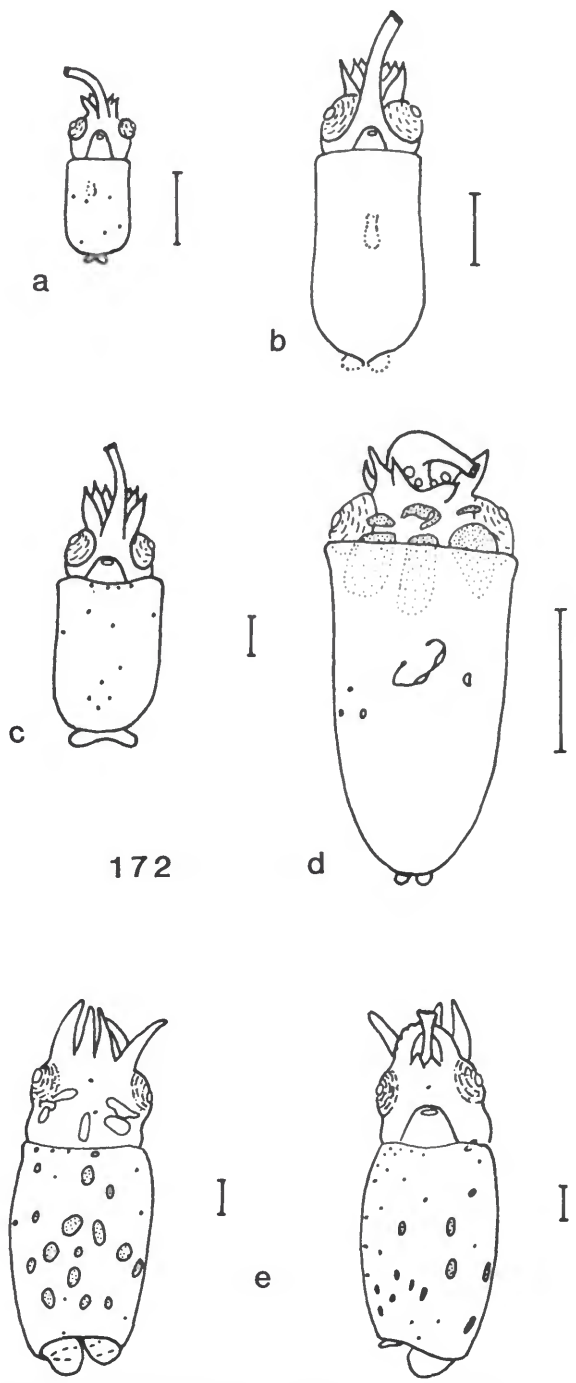
REFERENCES.—Nesis (1983), Roper et al. (1984), Wormuth (1976).

Hyaloteuthis Gray, 1849

GENERIC CHARACTERS.—Monotypic genus; see species.

Hyaloteuthis pelagica (Bosc, 1802)

SPECIES CHARACTERS.—*Adults:* Fin length 37% ML, width 58% ML, fin angle 50°; ventral surface of mantle covered with 19 relatively large, round light organs in a symmetrical pattern, usually in pairs; 3 round light organs along ventral surface of arms IV.



172

FIGURE 172.—*Dosidicus gigas*, southeastern Pacific. Growth series with chromatophore pattern. Scale bar = 1.0 mm. (From Nesis, 1983.)

Young (Figure 173): Single, round photophore on ventral surface of each eye (≥1.4 mm ML); single photophore centrally

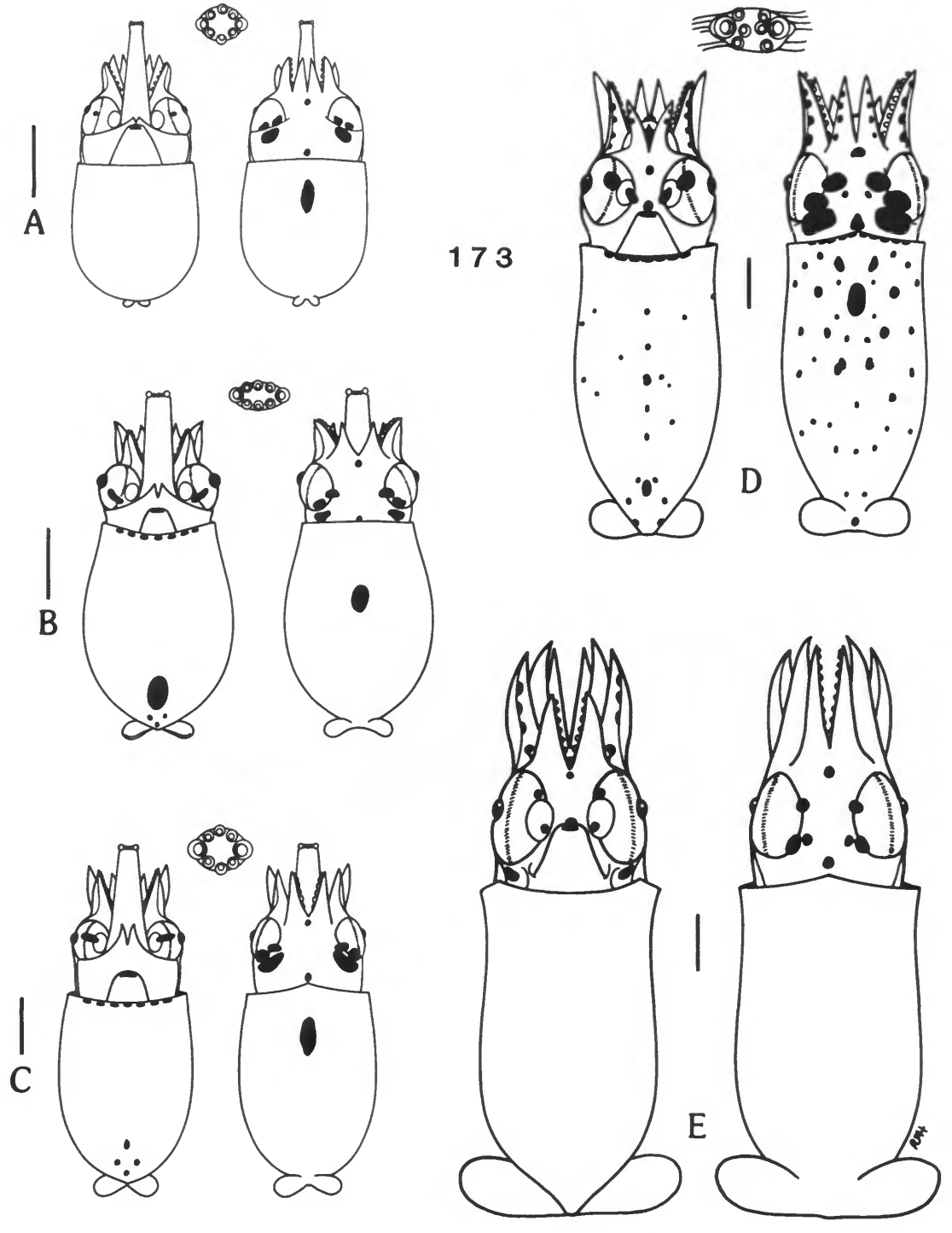


FIGURE 173.—*Hyaloteuthis pelagica*, dorsal and ventral views of larval stages, Hawaiian waters: *a*, 2.0 mm ML; *b*, 3.0 mm ML; *c*, 3.7 mm ML; *d*, 6.2 mm ML; *e*, 6.5 mm ML. Inserts show proboscis tips. Scale bar = 1.0 mm. (From Harman and Young, 1985.)

located on intestine (≥1.4 mm ML); mantle chromatophore pattern, when evident, shown in Figure 173*b–d;* proboscis length typically 50%–75% ML (<4 mm ML); proboscis length approximately equal or slightly longer than longest arms; lateral (distal) 2 suckers on proboscis tip 125%–150% that of remaining 6 suckers (Figure 173 inserts); division of proboscis begins at ~3.5–4.0 mm ML and tentacles separated at 6.0–6.5 mm ML.

GEOGRAPHICAL DISTRIBUTION.—Atlantic and Pacific Oceans (?Indian Ocean), tropical/subtropical.

VERTICAL DISTRIBUTION.—Oceanic, from surface to about 200 m.

REFERENCES.—Dunning and Brandt (1985), Harman and Young, (1985), Nesis and Nigmatullin (1979), Wormuth (1976).

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Family THYSANOTEUTHIDAE Keferstein, 1866

(by S.J. Stephen)

FAMILY CHARACTERS.—*Adults:* Rhomboidal fins extend length of mantle; powerful muscular mantle; funnel locking-cartilage with short, broad, transverse groove and long, narrow, longitudinal groove (sideways T-shape) (Figure 174*f*); long, slender trabeculae on protective membranes of arms.

Young (3 mm ML) (Figures 174*c,e*, 175): Sideways T-shape funnel locking-cartilage; small, broadly separated eyes that protrude in specimens smaller than 5 mm ML; mantle stout, short; dense concentration of small and large chromatophores on head, mantle, and arms; tentacles short, stouter and longer than arms at 1.5 mm ML, attenuate by 5 mm ML; arms with trabeculate protective membrane by 10 mm ML; fins small and rounded at 1.5 mm ML, but by 14 mm ML, fin length 64% ML (Yamamoto and Okutani, 1975).

Eggs: One of the few oegopsid families in which the spawn is known. Egg mass of *Thysanoteuthis* a gelatinous, sausage-shape, 600–1500 mm long by 100–200 mm diameter; contains a double row of eggs embedded in superficial layer of mass (Figure 179*a,b,d*) (Misaki and Okutani, 1976).

REMARKS.—The adult can reach 1000 mm ML. A second genus, *Cirrobrachium*, is described, but its validity has not been verified.

Thysanoteuthis Troschel, 1857

GENERIC CHARACTERS.—Family is presently considered monotypic; generic characters as given for family.

Thysanoteuthis rhombus Troschel, 1857

SPECIES CHARACTERS.—Those of the family.

GEOGRAPHICAL DISTRIBUTION.—Known worldwide from warm and temperate seas, particularly Mediterranean, Atlantic from Bermuda to South Africa, and Northwest Pacific around Japan (Clarke, 1966). Egg mass reported from Japan (Misaki and Okutani, 1976).

VERTICAL DISTRIBUTION.—Young and adults occur near the surface and have been reported to jump aboard vessels.

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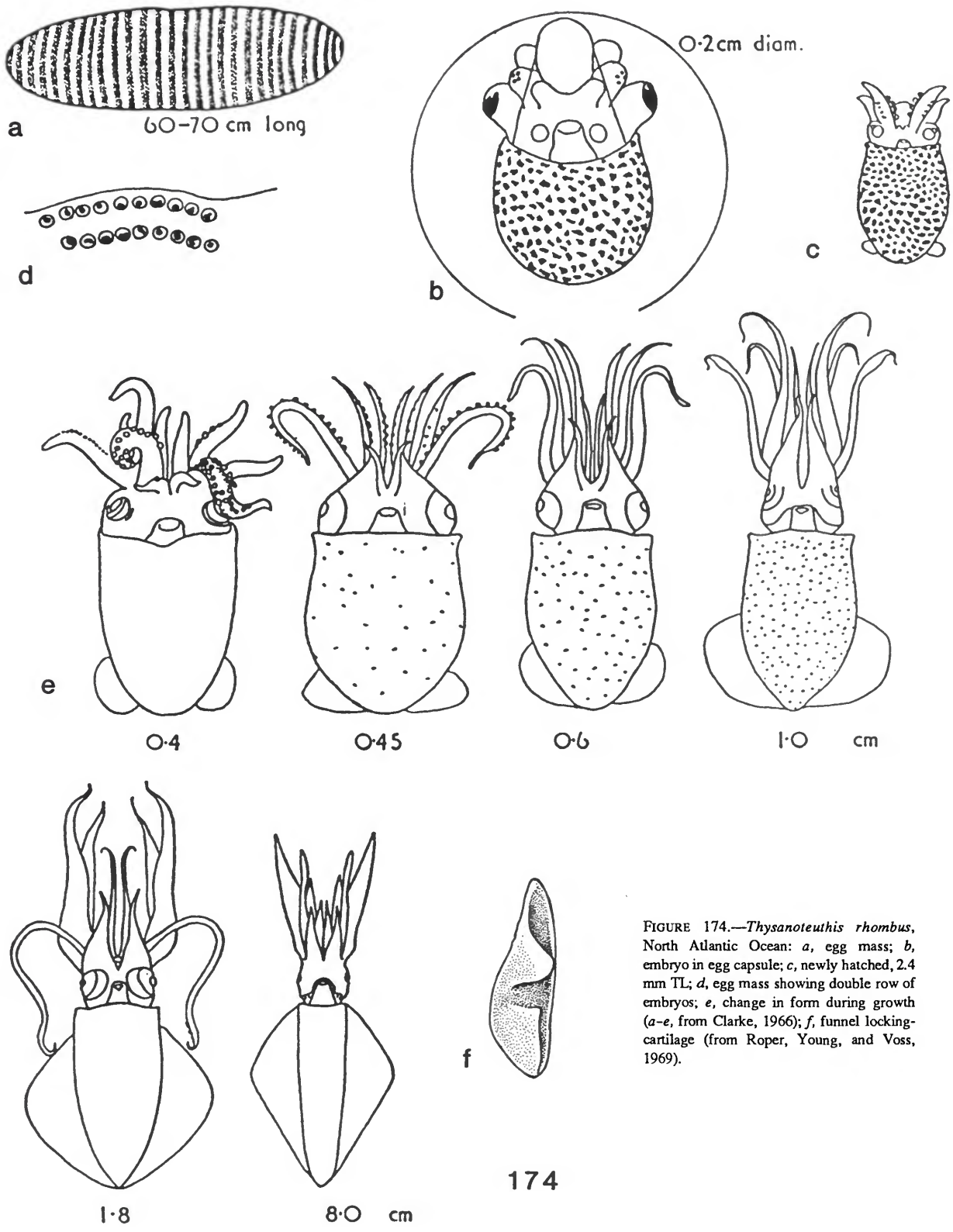

FIGURE 174.—*Thysanoteuthis rhombus*, North Atlantic Ocean: *a*, egg mass; *b*, embryo in egg capsule; *c*, newly hatched, 2.4 mm TL; *d*, egg mass showing double row of embryos; *e*, change in form during growth (*a–e*, from Clarke, 1966); *f*, funnel locking-cartilage (from Roper, Young, and Voss, 1969).

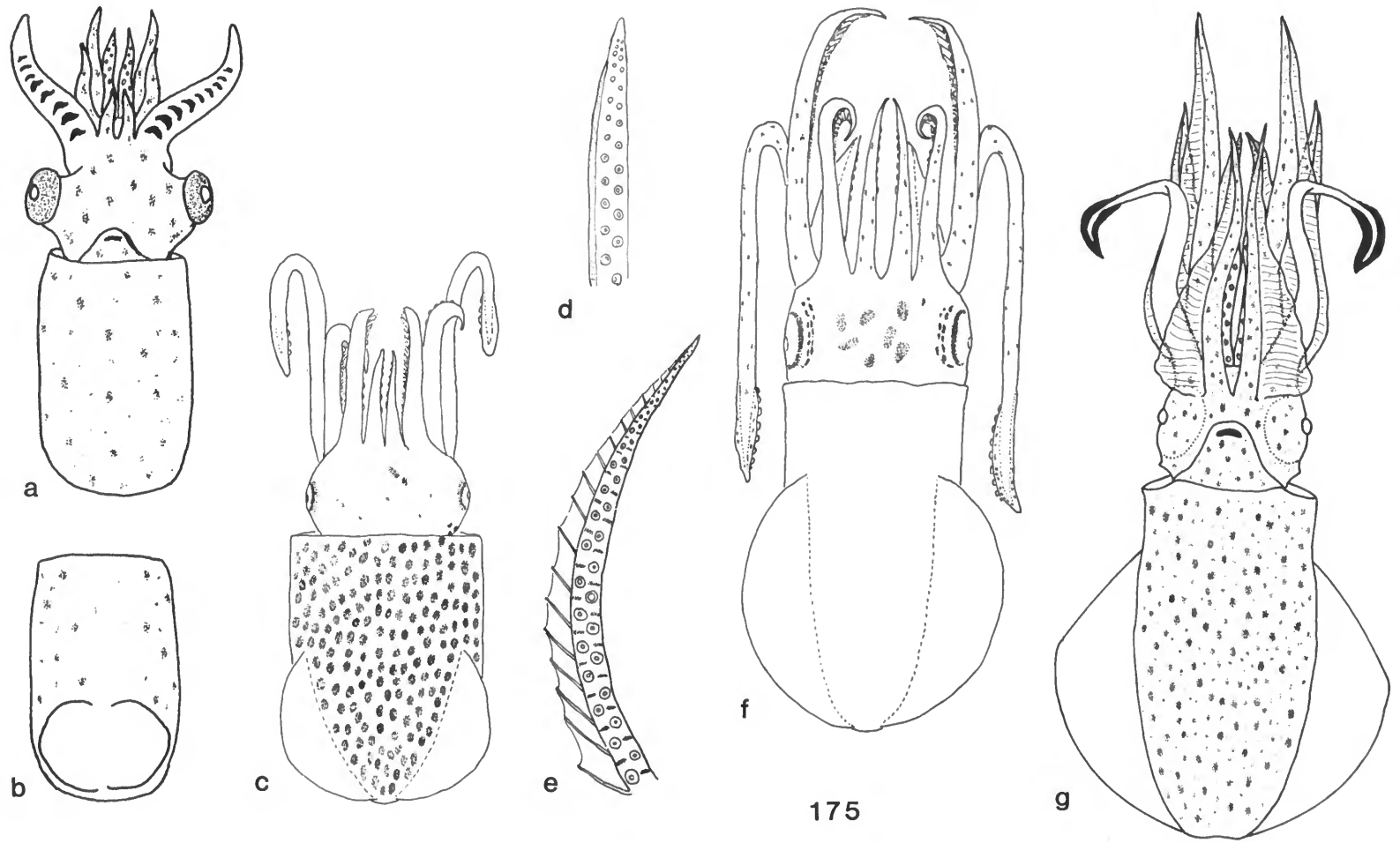

FIGURE 175.—*Thysanoteuthis rhombus: a,b,* 3 mm ML, Hawaiian waters (original drawings): *a,* ventral view; *b,* dorsal view. *c,d,* 5.5 mm ML, western North Pacific: *c,* dorsal view; *d,* right arm III. *e, f,* 10.5 mm ML, western North Pacific: *e,* right arm III; *f,* dorsal view (*c–f,* from Yamamoto and Okutani, 1975). *g,* 14 mm ML, NW Shelf Australia, ventral view (original drawing).

Family CTENOPTERYGIDAE Grimpe, 1922

(by K. Jefferts)

FAMILY CHARACTERS.—*Adults:* Fins extend along all or most of mantle length; fins consist of muscular trabeculae joined by a membrane; suckers on buccal membrane lappets; 8–14 rows of suckers on tentacular club; 4–6 rows of suckers on distal halves of arms I–III; buccal connectives attach to ventral borders of arms IV; straight, simple funnel locking-cartilage; in some species, photophores on ventral surface of ink sac; photophore dorsal to testis present in mature males of *Ctenopteryx sicula* (Young and Mangold, pers. comm.).

Young (Figure 176): Club suckers in distinctive circular pad (at <4 mm ML), pointed tip develops and becomes dactylus (at >4 mm ML), equals length of manus (at 6 mm ML); single chromatophore occurs on aboral surface of club (at ≥2 mm ML); fins separate dorsally, fringe mantle laterally; hatchlings with transversely elongate fins, result of first trabeculae; fins clearly with muscular trabeculae (at 3.5 mm ML); fin length increases with size; eyes small, widely separated.

Note: In hatchling (~1 mm ML) broad, oval club forms most of tentacle; from hatchling onward clubs very distinctive (at least in preserved specimens), bent laterally outward with sucker surfaces directed anteriorly.

REMARKS.—The family is monotypic.

Ctenopteryx Appellof, 1889

GENERIC CHARACTERS.—*Young:* Generic characters as for family.

GEOGRAPHICAL DISTRIBUTION.—Broad distribution worldwide from the Mediterranean, North and South Atlantic between about 40°N and 40°S, North and West Pacific (Clarke, 1966; Yamamoto and Okutani, 1975).

REMARKS.—The distinctive club and the fin trabeculae allow identification at all sizes. The several nominal species probably all belong to either the widely distributed *Ctenopteryx siculus* (Verany, 1851) or the poorly known *C. sepioloides* Rancurel, 1970, currently recorded only from the southwestern Pacific.

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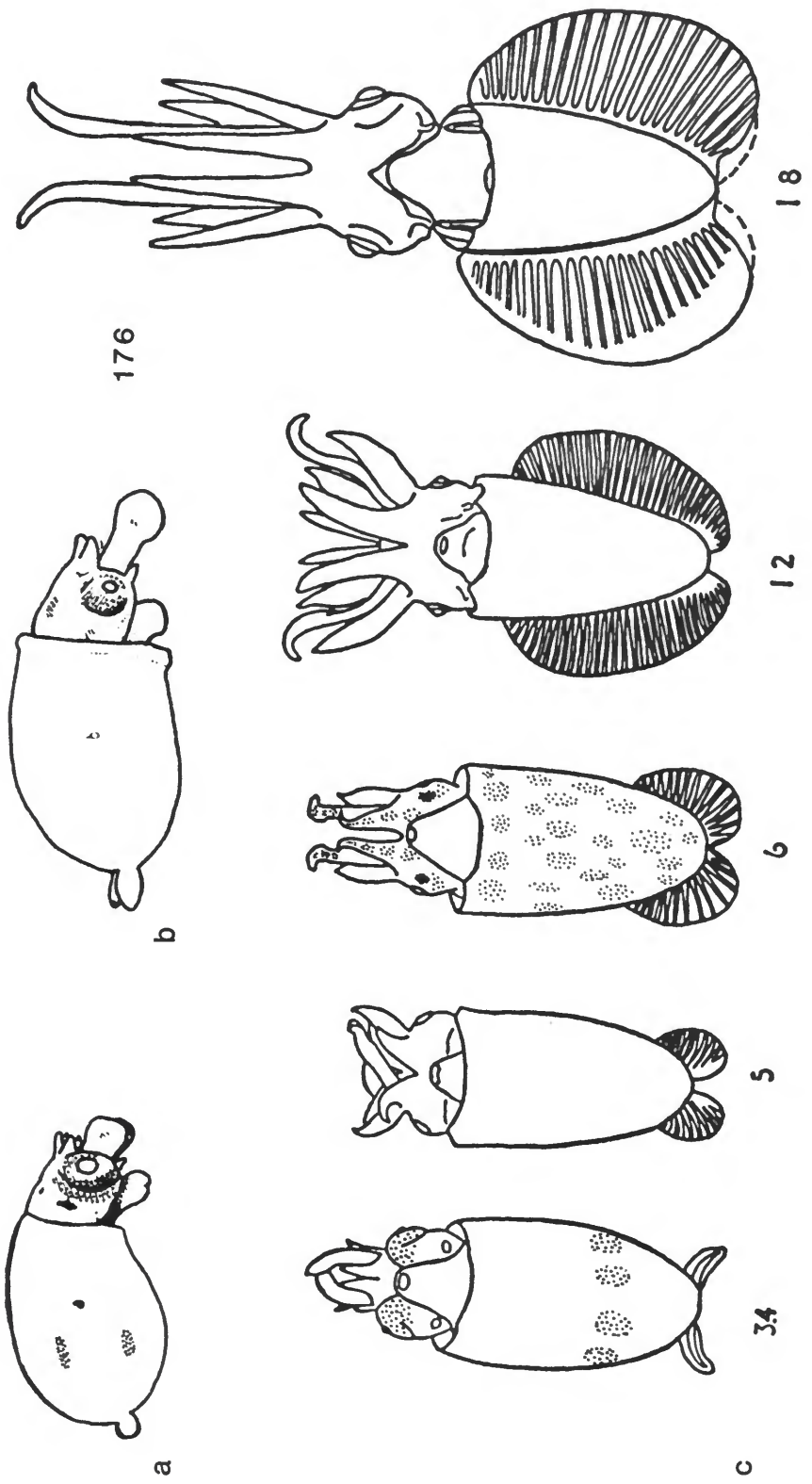

FIGURE 176.—*Ctenopteryx siculus*, Mediterrancan Sea: *a*, lateral view, 1.7 mm ML; *b*, lateral view, 2.0 mm ML (*a,b*, from Naef, 1923); *c–g*, ventral view of change in form during growth (from Clarke, 1966). Mantle lengths indicated in mm.

Family ONYCHOTEUTHIDAE Gray, 1849

(by M.R. Clarke)

FAMILY CHARACTERS (Figure 177).—*Adults:* Body muscular (in some species, postspawning specimens with soft mantle, possibly with soft papillae or wrinkles peripheral to muscle layers; mantle elongate, generally pointed posteriorly; arms with 2 rows of suckers; tentacular club with 2 rows of hooks with or without marginal suckers; distinct carpus comprised of oval pad with several rows of suckers and knobs; funnel locking-cartilage with straight groove (may slide on longer mantle ridge so that head partly withdraws into mantle in some species); mantle cartilages project anteriorly on either side of funnel; photophores absent in integument of mantle, head, and arms, may be present on viscera and/or eyes.

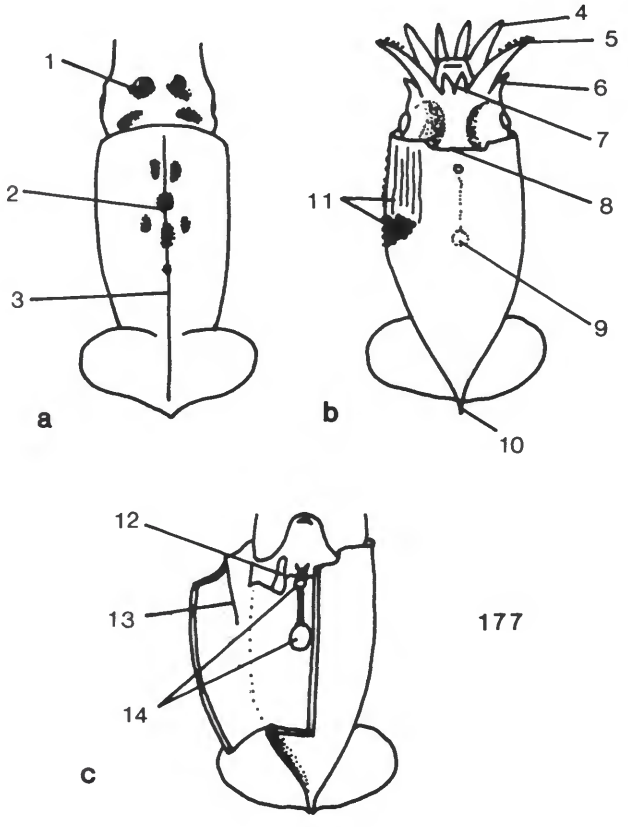

FIGURE 177.—Onychoteuthidae, schematic drawing to show features present in various members of the family: *a*, dorsal view; *b*, ventral view; *c*, ventral view with mantle opened: 1, large chromatophores on head; 2, large chromatophores on mantle; 3, gladius visible in dorsal midline; 4–7, relative sizes of arms I, II, III, tentacles, and IV; 8, mantle edge between connectives; 9, photophores on intestine; 10, protruding rostrum of gladius, "spike"; 11, wrinkling or papillation of mantle surface; 12, elongate funnel connective; 13, long mantle connective; 14, photophores ventral to intestine. (Original drawings.)

Young: (Figures 177, 178): Mantle relatively broad in youngest stages but sharply pointed posteriorly, often constricted anteriorly relative to midpoint, especially in youngest stages; mantle surface often with fine longitudinal wrinkling of its outer layer; head often withdrawn into mantle up to eye lenses and tip of funnel in some species; tentacles thick and slightly longer than arms I and II; large, dark chromatophores may occur on dorsal mantle and head.

Eggs: Spawn of species in this family not positively identified; large nidamental glands suggest eggs laid in large gelatinous masses.

REMARKS.—Certain features that clearly distinguish species in adults appear early in development, but the material available for study is insufficient to determine the mantle length at which most of them appear. However, such features often are useful in distinguishing juveniles. Therefore, the diagnoses of species given below are not divided into "Adults" and "Young" as in other chapters (exceptions are species described from Hawaiian Islands material). The characters are for adults, juveniles, or young and can be used in "working backward" to identify younger and younger forms. Naef (1923) gives a detailed description of postembryonic development.

Key to the Genera and Most Species of ONYCHOTEUTHIDAE*

1. Antarctic south of 50°S, probably south of Antarctic Convergence 2
   15°S to 40°S 3
   Tropical and temperate, 15°S to 40°N 5
   North of 30°N in Pacific 8
2. Smooth mantle surface; 30 club hooks or less; less than 16 suckers on dactylus; no marginal club suckers . . . . . ***Moroteuthis knipovitchi***
   Wrinkled mantle surface at 3 mm ML; 30 club hooks or more; more than 24 suckers on dactylus; marginal suckers present on club . . . . ***Kondakovia longimana***
3. Large, dark chromatophores on dorsal mantle midline at <2 mm ML; club hooks differentiate at <10 mm ML . . . . . ***Onykia carribaea***
   Chromatophores less obvious; club hooks differentiate at >10 mm ML 4
4. Photophores on eyes and intestine visible at 11 mm ML . . . . . ***Onychoteuthis banksi*** complex
   No photophores on eyes and intestine . . . . . ***Moroteuthis robusta*** and ***Moroteuthis ingens***
5. Photophores on eyes and intestine visible at 11 mm ML . . . . . ***Onychoteuthis banksi*** complex
   No photophores on eyes and intestine 6
6. Large, dark chromatophore on dorsal mantle at <2 mm ML; club hooks differentiate at <10 mm ML . . . . . ***Onykia***
   Chromatophores less obvious; club hooks differentiate at >10 mm ML 7

7. Nuchal folds present on head . . . . . *Ancistroteuthis*
   Nuchal folds absent . . . . . *Moroteuthis aequatorialis*
8. Photophores on eyes and intestine visible at 11 mm ML . . . . . *Onychoteuthis borealijaponica*
   No photophores on eyes and intestine 9
9. More than 30 club hooks; body surface with longitudinal wrinkles 10
   Fewer than 20 club hooks; body smooth or with papillae 11
10. Small species, known to grow to 160 mm ML . . . . . *Moroteuthis pacifica*
    Large species, grows to over 1000 mm ML . . . . . *Moroteuthis robusta*
11. 18 club hooks, body surface smooth . . . . . *Moroteuthis japonica*
    13 club hooks; body surface with papillae . . . . . *Moroteuthis lonnbergi*

*Key based largely on known geographical distribution and on late juvenile features, but may aid in identification of early juveniles.

Onychoteuthis Lichtenstein, 1818

GENERIC CHARACTERS (Figure 178).—Muscular mantle and head usually smooth; nuchal folds present; several folds or pleats in skin radiate from posterodorsal (nuchal) region of

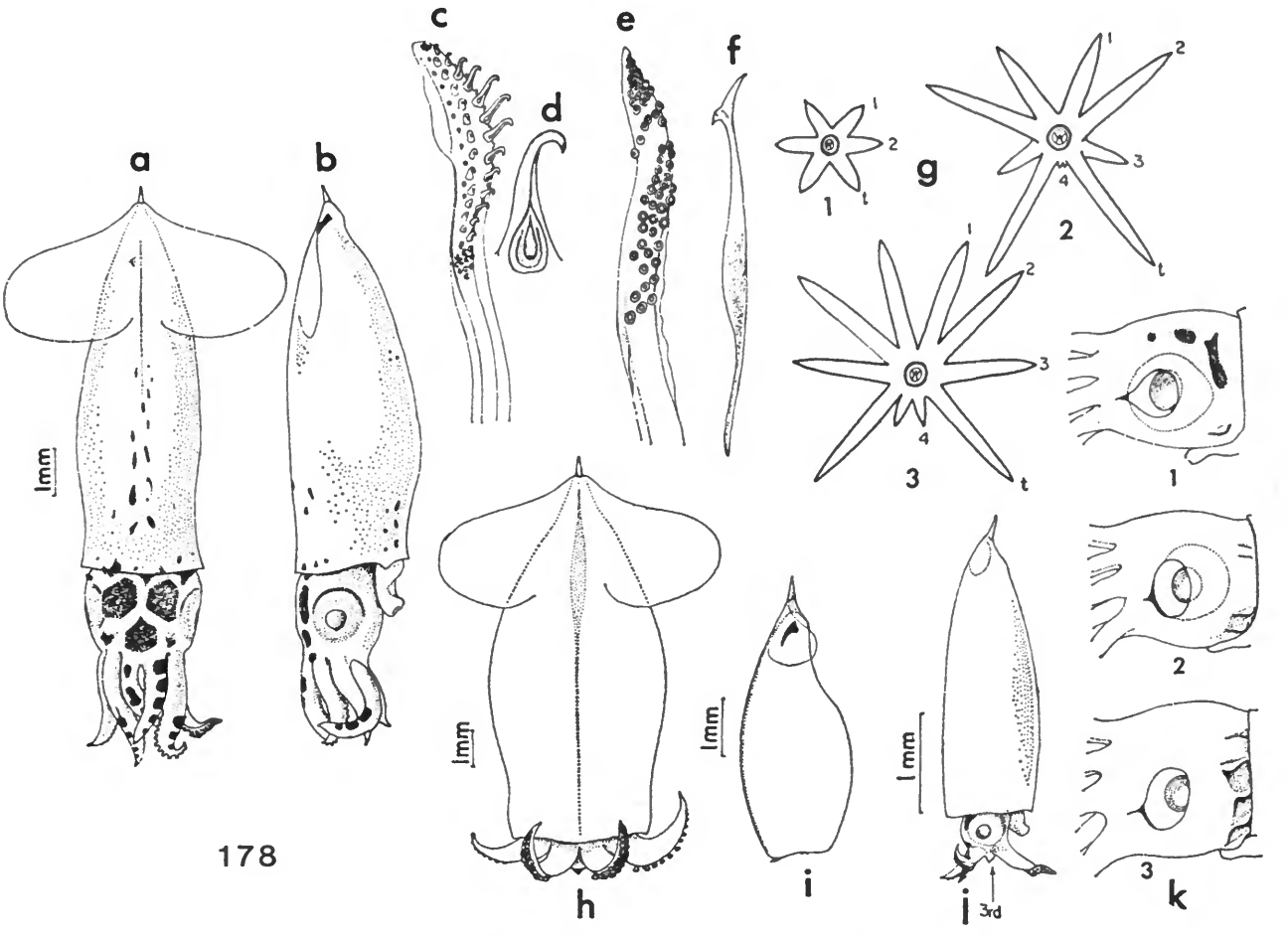

FIGURE 178.—*Onychoteuthis borealijaponica*, Californinia Current: *a*, dorsal view; *b*, lateral view of *a*; *c*, tentacle of juvenile; *d*, tentacular hook from *c*; *e*, tentacular club, <20 mm ML larva; *f*, gladius, 3 mm ML; *g*, diagram of development of arms and tentacles (1, 3.1 mm ML; 2, 5.5 mm ML; 3, 8.0 mm ML); *h*, dorsal view of juvenile with head withdrawn into mantle cavity; *i*, lateral view of individual younger than *h* (head withdrawn and tips of arms just visible); *j*, lateral view of young individual showing relative size of third arms; *k*, development of olfactory crests: ventral-most crest develops first (1), followed by second ventral and beginning of two dorsal crests (2), and then medial crest develops (3). (From Okutani and McGowan, 1969.)

head; marginal suckers on tentacles lost at early stage; 19–27 club hooks (largest hooks clearly differentiated at 12 mm ML); carpal pad with 6–10 suckers and knobs; 2 photophores on viscera, 1 dorsal to intestine and 1 ventral to ink gland and duct (visible at 11 mm ML); 1 patch of photogenic tissue (developing photophore) on ventral surface of each eye; gladius with pointed rostrum, diagonally directed dorsally, extends past end of mantle as characteristic spike; gladius visible as dark line running length of dorsal mantle; conus well devloped, deep; medium size squids to about 300–400 mm ML.

REMARKS.—*Onychoteuthis* greater than 11 mm ML can be distinguished from *Ancistroteuthis* by (a) significantly larger fins, greater than 30% ML; (b) gladius visible dorsally as distinct line; (c) tentacular club hooks differentiated at a slightly greater ML; (d) presence of photophores.

REFERENCES.—Naef (1923), Nesis (1973), Okutani and McGowan (1969), Okutani and Murata (1983), Roper et al. (1984), Yamamoto and Okutani (1975), Young (1972), Young and Harman (1987).

Onychoteuthis banksi complex (Leach, 1817)

SPECIES CHARACTERS.—19–23 hooks on tentacular clubs; 4 rows of suckers on distal end of tentacular club and 2 rows over most of tentacular stalk at 3 mm ML (Naef, 1923; Young, 1972).

GEOGRAPHICAL DISTRIBUTION.—Widespread in all oceans from 40°N to southern subtropical convergence near 40°S. Probably extends to polar regions in North Atlantic.

REMARKS.—Included under this name are a complex of several species (Young, 1972; Young and Harman, 1987).

Onychoteuthis borealijaponica Okada, 1927

SPECIES CHARACTERS (Figure 178).—25–27 hooks on tentacular clubs; hooks appear at 30 mm ML.

GEOGRAPHICAL DISTRIBUTION.—North Pacific, 30°N to 55°N.

REMARKS.—Juveniles misidentified by Okutani and McGowan (1969) as *O. banksii* are this species (Yamamoto and Okutani, 1975).

Onychoteuthis compacta (Berry, 1913)

SPECIES CHARACTERS.—*Young* (Figure 179): Head usually partially or fully retracted into mantle cavity (Figure 179*a–c*); ocular photophores present by 9–10 mm GL; arms and tentacles short; ventral series of club hooks first appear at 12–14 mm GL, dorsal series not present in 20.5 mm GL specimen, but hook rudiments present in 21.5 mm GL specimen; several small chromatophores broadly scattered on posterior third of ventral surface of mantle at <4–5 mm GL (Figure 179*b,c*); 10–15 small chromatophores arranged in 2 longitudinal rows present along middorsal line of mantle by 9 mm GL (Figure 179*d*); visceral photophores present by 9–10 mm GL; fins large.

GEOGRAPHICAL DISTRIBUTION.—Presently recorded only from Hawaiian Islands.

VERTICAL DISTRIBUTION.—Taken at 50–150 m during the day and upper 25 m at night; data for October only.

Onychoteuthis species B, Young and Harman, 1987

SPECIES CHARACTERS.—*Young* (Figure 180): Head rarely retracted into mantle cavity (Figure 180*a–c*); posterior component of ocular photophores present by 3–4 mm GL, anterior component appears at 5–7 mm GL; arms and tentacles long; ventral series of club hooks appears at 7–8 mm GL, dorsal series not present in 16 mm GL specimen; numerous ventral mantle (belly) chromatophores occur in 1.8–2.0 mm GL specimens (Figure 180*a*); dorsal mantle chromatophores on midline, usually form single, straight row (Figure 180*b*) (sometimes with few additional nonaligned chromatophores by 3.5–4.0 mm GL); visceral photophores present by 5–6 mm GL; fins large.

GEOGRAPHICAL DISTRIBUTION.—Presently recorded only from Hawaiian Islands.

VERTICAL DISTRIBUTION.—Taken in upper 100 m during day and night; data for October only.

REFERENCES.—Young and Harman (1987).

Onychoteuthis species C, Young and Harman, 1987

SPECIES CHARACTERS.—*Young* (Figure 181): Head rarely retracted into mantle cavity (Figure 181*a,b*); posterior component of ocular photophores present at 4–5 mm GL, anterior component present at 7–8 mm GL; arms and tentacle intermediate in length; ventral series of club hooks first appear at 8–10 mm GL, dorsal series present in 17 mm GL specimen; ventral mantle (belly) chromatophores form single band in 2.5 mm GL specimen (Figure 181*a*), often 2 irregular bands by 5–6 mm GL (Figure 181*b*); dorsal mantle (midregion) chromatophores along midline in complex row or patch in <6 mm GL specimens (Figure 181*b*); visceral photophores present by 5–7 mm GL; fins short.

GEOGRAPHICAL DISTRIBUTION.—Presently recorded only from Hawaiian Islands.

VERTICAL DISTRIBUTION.—Taken in 50–150 m during day and upper 50 m during night; data for April and October only.

REFERENCES.—Young and Harman (1987).

Onykia Lesueur, 1821

GENERIC CHARACTERS.—Surface of mantle and head usually smooth; nuchal folds absent; marginal suckers on tentacular club retained throughout life; in young juveniles tentacular club suckers in 2 rows over much of tentacle length, then in 4 rows, before formation of club per se; photophores

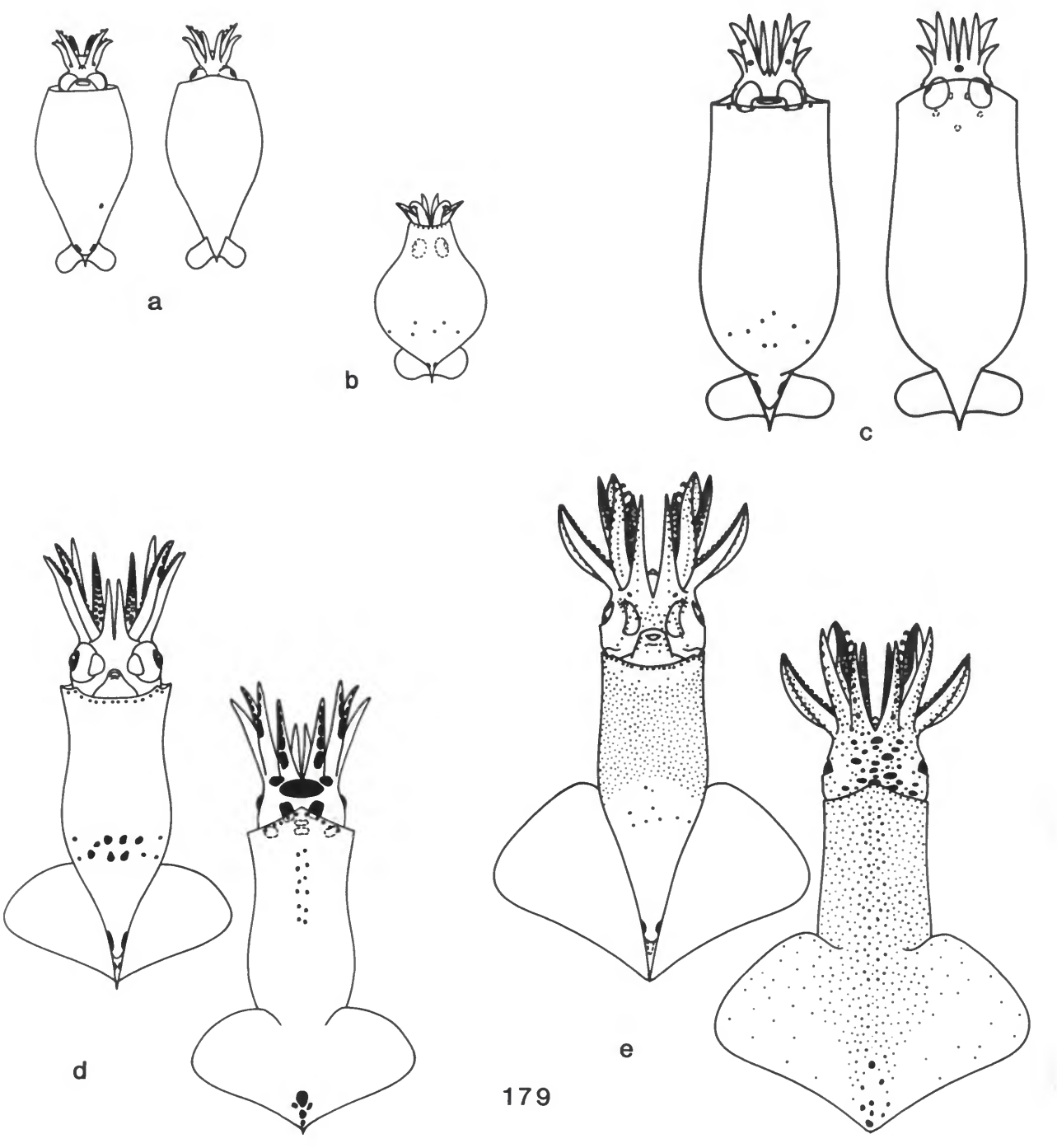

FIGURE 179.—*Onychoteuthis compacta,* Hawaiian waters: *a,* ventral and dorsal views, 2.3 mm GL larva; *b,* ventral view, 4.8 mm GL larva with head retracted; *c,* ventral and dorsal views, 4.1 mm GL larva; *d,* ventral and dorsal views, 8.9 mm GL larva; *e,* ventral and dorsal views, 18.5 mm GL juvenile. Dotted circles in *c,d* represent head chromatophores. (From Young and Harman, 1987.)

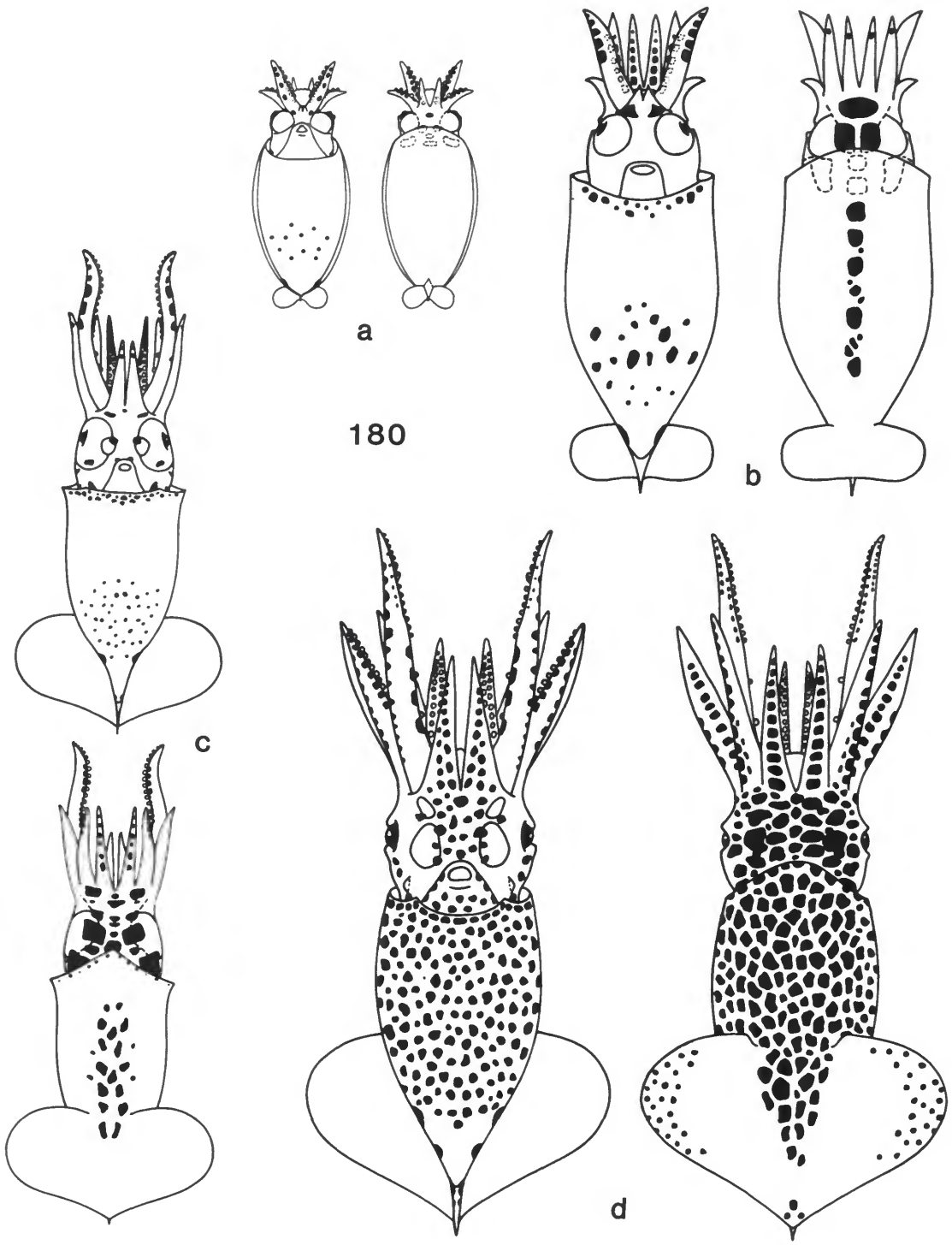

FIGURE 180.—*Onychoteuthis* sp. *B*., ventral and dorsal views of growth series from Hawaiian waters: *a*, 1.9 mm GL larva; *b*, 3.8 mm GL larva; *c*, 5.8 mm GL larva; *d*, 8.8 mm GL juvenile. (From Young and Harman, 1987.)

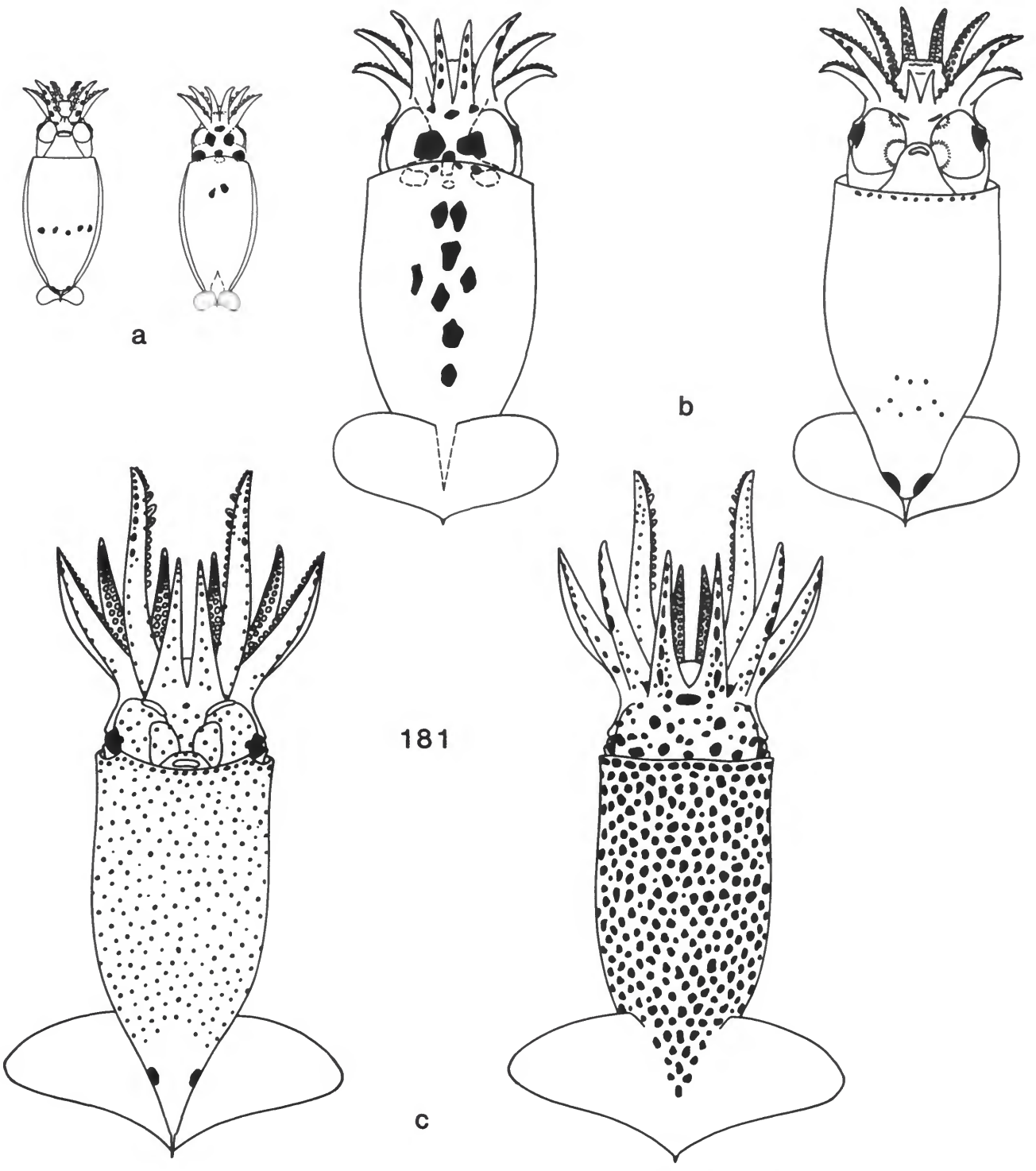

FIGURE 181.—*Onychoteuthis* sp. *C.*, ventral and dorsal views of growth series from Hawaiian waters: *a*, 2.2 mm GL larva; *b*, 5.2 mm GL larva; *c*, 9.6 mm GL juvenile. (From Young and Harman, 1987.)

absent; mantle, head, funnel, arms, and tentacles all densely covered with chromatophores at about >3 mm ML; larvae with characteristic dark chromatophores along dorsal midline when expanded, and increase in size from anterior to posterior; mantle not as sharply pointed posteriorly as in *Onychoteuthis*, more bullet-shape; small broad-bodied squids growing to 68 mm ML (Okutani, 1981).

REMARKS.—This genus needs revision. While the young of *Onykia carribaea* (Figure 182) have been described previously, no description is given here because *O. carribaea* now is known to be a species complex that must be sorted out at the adult level first. See Taki (1964) for discussion on generic name and priority.

Onykia carribaea (Lesueur, 1821)

SPECIES CHARACTERS.—See above.

GEOGRAPHICAL DISTRIBUTION.—Atlantic from 45°N to 40°S and at similar latitudes in Pacific and Indian Oceans (Clarke, 1966).

VERTICAL DISTRIBUTION.—Squids often live close to sea surface but may occur as deep as 200 m.

REMARKS.—Freshly caught specimens may display a distinct blue sheen dorsally.

Onykia rancureli Okutani, 1981

SPECIES CHARACTERS.—Club with 3–4 marginal suckers on each side of manus, 10–13 hooks, 9 carpal suckers; grows to at least 103 mm GL.

GEOGRAPHICAL DISTRIBUTION.—Tropical Indian and Pacific Oceans.

Onykia indica Okutani, 1981

SPECIES CHARACTERS.—Broad fin angled at ends; arms very long, slender; club with 3–4 marginal suckers on each side of manus, 7 carpal suckers, 12–13 hooks; grows to at least 33 mm GL.

GEOGRAPHICAL DISTRIBUTION.—Eastern Indian Ocean.

Ancistroteuthis Gray, 1849

GENERIC CHARACTERS.—Surface of muscular mantle and head smooth; nuchal folds present; gladius not visible along dorsal midline; conus consists of minute spoon (not a deep conical end part as in *Onychoteuthis*) and long cartilaginous rostrum, 1/7 gladius length; fins longer than 1/3 ML at 16 mm ML; carpal pad with 8–12 suckers and knobs; photophores absent.

REMARKS.—This genus can be differentiated from *Onychoteuthis* above 11 mm ML; see Remarks under *Onychoteuthis*. Also see Naef (1923) for detailed description of juveniles.

Ancistroteuthis lichtensteini (Orbigny, 1839)

SPECIES CHARACTERS.—With characters of genus.

GEOGRAPHICAL DISTRIBUTION.—Western Mediterranean, West Africa (11°S, 14°E), and possibly Gulf of Mexico and Melanesia.

REMARKS.—Mature specimens unknown.

REFERENCES.—Adam (1962), Naef (1923), Voss (1956).

Chaunoteuthis Appellof, 1891

REMARKS.—This genus probably was based on spent female *Onychoteuthis* or *Ancistroteuthis* specimens that, in common with other onychoteuthid species (and some other oegopsids), become gelatinous and flaccid and change proportions after laying eggs (Clarke, 1980). Naef (1923), however, described a larva (12.5 mm ML) differing from *Onychoteuthis banksi* only in having gelatinous tissues, the middle of the gladius covered in muscle, and a smaller funnel. The validity of the genus needs verification. Adam (1972) suggests that *Chaunoteuthis* and *Onychoteuthis* are synonymous, a view shared by several workers.

REFERENCES.—Adam (1972), Clarke (1980), Naef (1923).

Moroteuthis Verrill, 1881

GENERIC CHARACTERS (Figure 183).—Surface of muscular mantle overlain by soft papillae or longitudinal ridges (gelatinous in larger specimens) in all but *M. knipovitchi;* nuchal folds absent; no marginal suckers on tentacular club in large specimens; 12–36 club hooks; no photophores on eye or intestine; posterior end of gladius extended by cartilaginous rostrum, gladius not visible as dark line along dorsum of mantle; carpal pad with 7–13 suckers and knobs; medium to large size squids, grows to about 1000 mm ML.

Moroteuthis robusta (Verrill, 1876)

SPECIES CHARACTERS.—Surface of muscular mantle covered by soft longitudinal ridges; 32–36 club hooks; 8–12 suckers on dactylus; 10–12 suckers and knobs on carpus; maximum ventral length of cartilaginous rostrum of gladius 29%–40% ML; largest specimens grow to about 1000 mm ML.

GEOGRAPHICAL DISTRIBUTION.—Pacific, Subarctic.

REFERENCES.—Clarke (1980), Roper et al. (1984).

Moroteuthis ingens (Smith, 1881)

SPECIES CHARACTERS.—Surface of mantle covered with round papillae by 6.5 mm ML; tentacular club with 28–32 hooks in 2 rows, 15–17 suckers on dactylus; 4 rows of suckers to base of tentacles at 6.5 mm ML; ventral length of cartilaginous rostrum of gladius 6%–10% ML; largest speci-

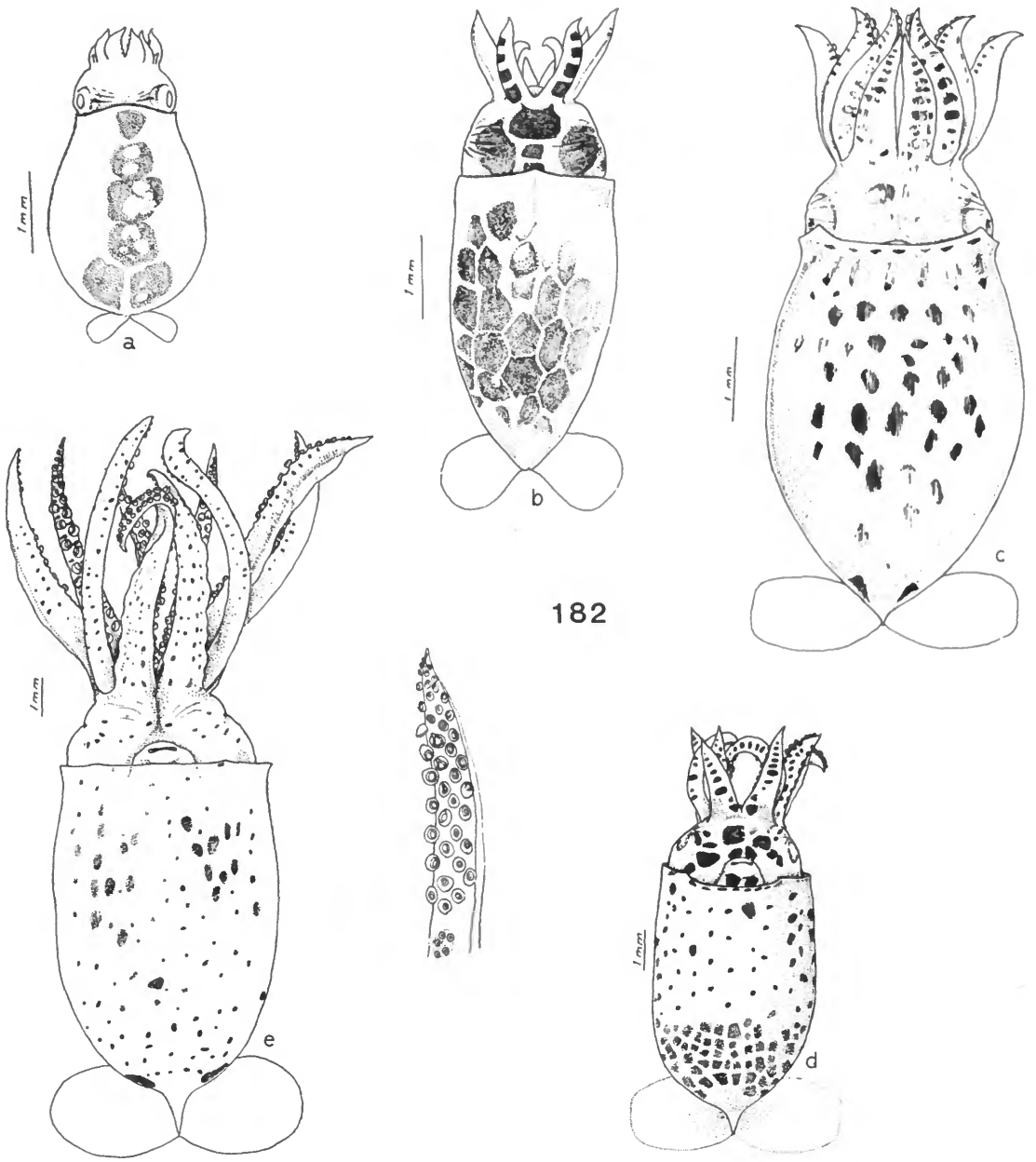

FIGURE 182.—*Onykia carribaea*, growth series and chromatophore development, western North Pacific. (From Yamamoto and Okutani, 1975.)

mens grow to about 400 mm ML.

GEOGRAPHICAL DISTRIBUTION.—Patagonia and off New Zealand; Subantarctic.

REMARKS.—Beaks of this species from sperm whale stomachs were identified as *Moroteuthis* A by Clarke (1980).

REFERENCES.—Clarke (1980), Roper et al. (1984).

Moroteuthis robsoni Adam, 1962

SPECIES CHARACTERS.—Surface of mantle covered by round papillae; 26–30 club hooks; 12–19 suckers on dactylus; 8–12 suckers and knobs on carpus; ventral length of cartilaginous rostrum of gladius 21%–36% ML; largest

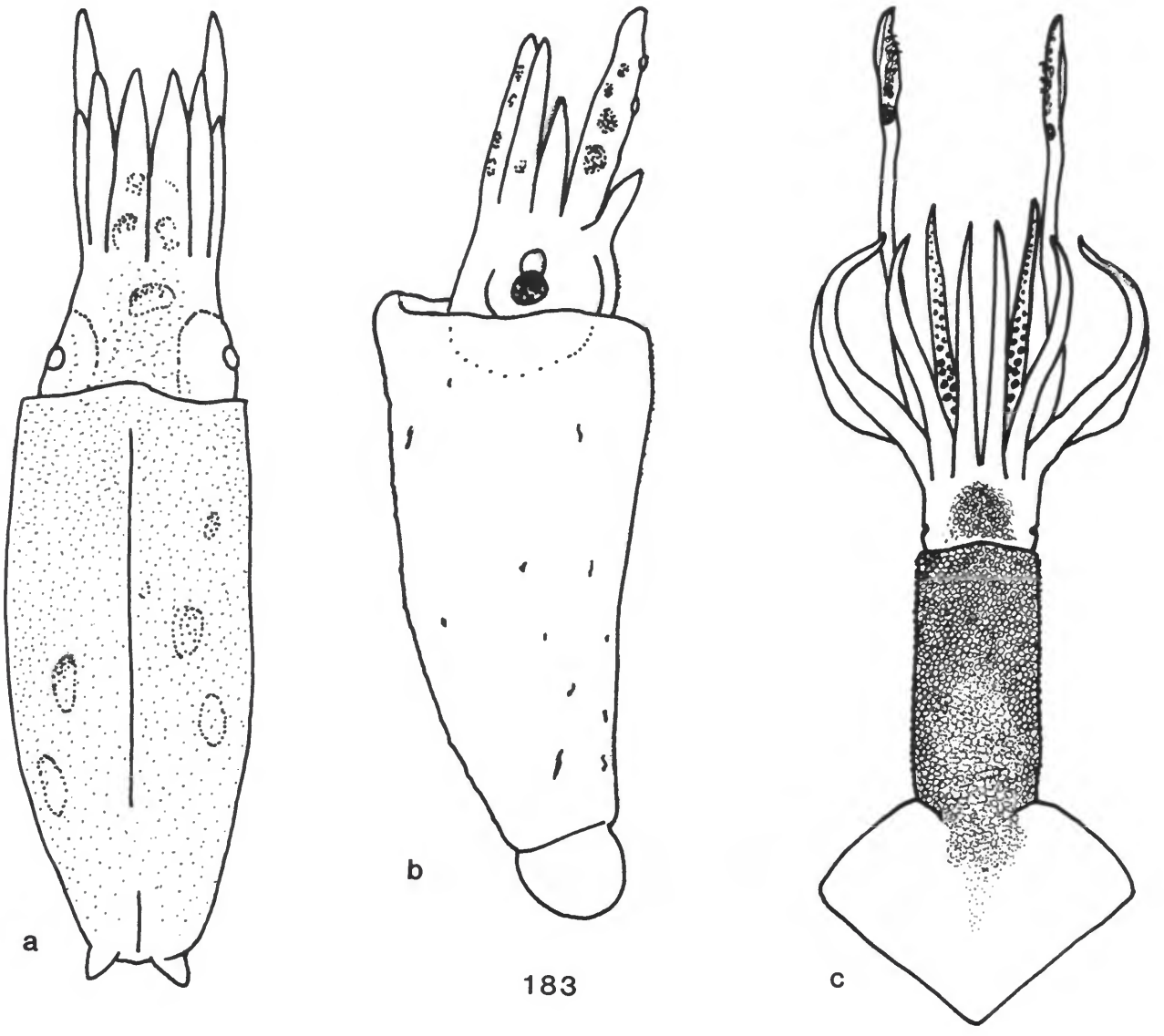

FIGURE 183.—*Moroteuthis: a,b,* 6 mm ML juvenile (original drawings): *a,* dorsal view; *b,* right lateral view. *c,* 38 mm ML adult, Patagonia, dorsal view. (Redrawn from Lonnberg, 1898.)

specimens grow to about 700 mm ML.

GEOGRAPHICAL DISTRIBUTION.—16°S to 47°S from South Georgia to New Zealand; probably circumglobal.

REFERENCES.—Clarke (1980), Clarke and MacLeod (1982).

Moroteuthis knipovitchi Filippova, 1972

SPECIES CHARACTERS.—Surface of mantle smooth; 20–30 club hooks; 14–16 suckers on dactylus; 9–13 suckers and knobs on carpus; ventral length of cartilaginous rostrum of gladius 10%–13% ML; largest specimens grow to about 320 mm ML.

GEOGRAPHICAL DISTRIBUTION.—Antarctic, probably circumpolar.

REFERENCES.—Clarke (1980).

Moroteuthis lonnbergi Ishikawa and Wakiya, 1914

SPECIES CHARACTERS.—Surface of mantle covered by round papillae; 13 club hooks; 10–14 suckers on dactylus; 7–8

suckers and knobs on carpus; ventral length of cartilaginous rostrum of gladius not recorded; largest specimens grow to about 300 mm ML.

GEOGRAPHICAL DISTRIBUTION.—Western Pacific off eastern Japan.

Moroteuthis aequatorialis Thiele, 1921

REMARKS.—Imperfectly known from only one specimen with no papillae on surface of mantle, caught at 0°16′N, 18°W in the tropical Atlantic; 400 mm ML.

Moroteuthis japonica (Taki, 1964)

SPECIES CHARACTERS.—Body muscular with smooth surface; 18 club hooks; 8 suckers and knobs on carpus.

GEOGRAPHICAL DISTRIBUTION.—Off Japan.

REMARKS.—Only one specimen (60 mm ML) has been described.

REFERENCES.—Okutani (1983).

Moroteuthis pacifica Okutani, 1983

SPECIES CHARACTERS.—Body muscular but soft, covered by longitudinal ridges or wrinkles; 30–34 club hooks; 14 suckers on dactylus; 11–13 suckers and knobs on carpus; ventral length of rostrum of gladius 25% ML; known to grow to 160 mm ML.

GEOGRAPHICAL DISTRIBUTION.—Pacific, 35°N to 40°N.

REFERENCES.—Okutani (1983).

Kondakovia Filippova, 1972

GENERIC CHARACTERS (Figure 184).—Monotypic; mantle with longitudinal ridges of soft tissue external to thick, soft muscle layer; marginal suckers and 2 rows of hooks on tentacular club.

Kondakovia longimana Filippova, 1972

SPECIES CHARACTERS.—Body muscular but soft with longitudinal wrinkles in soft outer layer at 3 mm ML; 30–38 club hooks; 4 rows of suckers to base of tentacle; 24–40 suckers on dactylus; 9–13 suckers and knobs on carpus at 4.7 mm ML; ventral length of cartilaginous rostrum of gladius 5%–12% ML; grows to larger than 750 mm ML.

GEOGRAPHICAL DISTRIBUTION.—Antarctic, probably circumpolar.

REMARKS.—Until 1972 this species was confused with *Moroteuthis ingens* (see Clarke, 1980). This species is a major food item of sperm whales.

REFERENCES.—Clarke (1980), Clarke and MacLeod (1983).

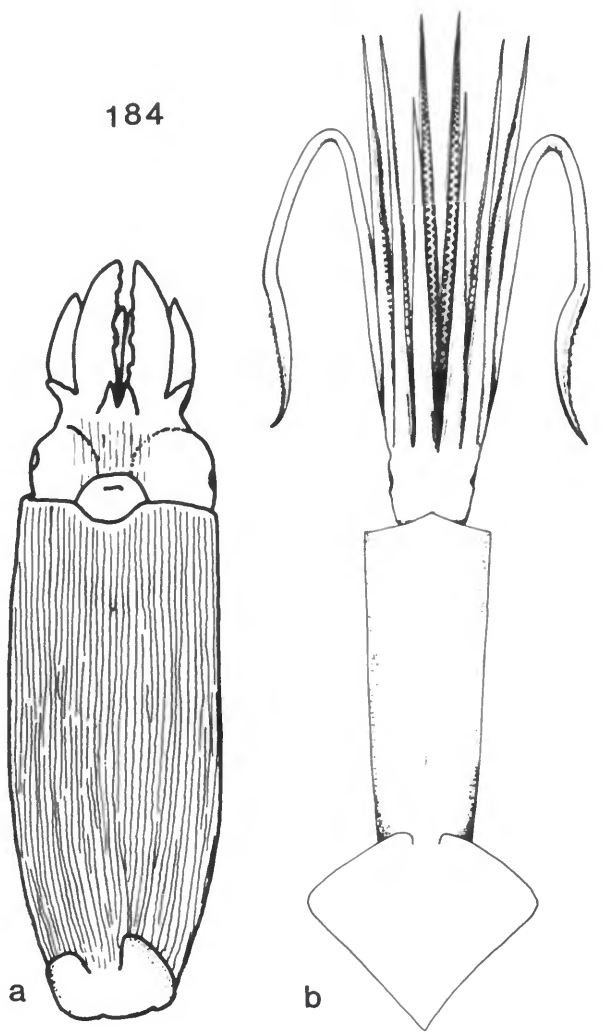

FIGURE 184.—*Kondakovia longimana*, Antarctic: *a*, ventral view, 5 mm ML, juvenile (original drawing); *b*, dorsal view, 700 mm ML, adult (from Clarke, 1980).

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Family GONATIDAE Hoyle, 1886

(by T. Okutani and M.R. Clarke)

FAMILY CHARACTERS.—*Adults:* Arms with 4 rows of suckers with some in medial rows developed into hooks on arms I-III in all genera and species except for *Berryteuthis* spp.; in one species of *Gonatopsis* 12 rows of suckers on tips of arms; simple, straight funnel locking-cartilage, groove of which may widen posteriorly; buccal connectives attach to ventral borders of arms IV; numerous irregular rows of suckers on tentacular club often with several enlarged (graded) hooks; photophores known in only one species.

Young: Characteristically head drawn into mantle up to level of eye lens in preserved condition; arms IV usually shorter than arms II and III; mantle usually emarginated between ventral mantle connectives; fins usually <20% ML at 10 mm ML, increasing in larger juveniles to <30% ML; tentacular clubs with >4 rows of minute suckers at 10 mm ML (may be fewer in *Gonatopsis*); few chromatophores in young juveniles; fins usually lobed anteriorly and extended posterior to short, pointed posterior end of mantle; developmental series in Okutani (1968, 1969).

GEOGRAPHICAL DISTRIBUTION.—The gonatid species are the most abundant squids in the Arctic waters and extend into subarctic waters and southward to about 35°N in the Pacific and Atlantic. One species occurs in the Antarctic and extends northward to 40°N. Summaries of geographical distribution of all life stages are given in Clarke (1966), Kubodera and Jefferts (1984), and Okutani, Kubodera, and Jefferts (1988).

VERTICAL DISTRIBUTION.—Adults at the surface in high latitudes; generally from surface to about 1000 m. Some species undergo diel vertical migrations, living at 400-800 m during the day and ascending to 100-400 m at night (Roper and Young, 1975). "Larvae" are most abundant in upper 200-300 m and are more common over the continental slope waters in summer (Pearcy, 1965). Lu and Clarke (1975) record vertical distribution of *Gonatus fabricii* wherein young <20.5 mm ML occur at depths <200 m and specimens above 20.5 mm ML are spread out between 10-1500 m, suggesting an ontogenetic descent.

REMARKS.—Three genera are recognized in the Gonatidae: *Gonatus, Gonatopsis,* and *Berryteuthis.* A subgenus, *Eogonatus,* has been described (Nesis, 1972). It was elevated to the generic level by Okutani et al. (1988), but in the absence of study material, its specific identity here is not considered further. Gonatids appear to be among the most abundant of all cephalopods in northern high latitudes.

Key to Genera of GONATIDAE

1. Tentacles absent in specimens >10-12 mm ML; specimens <10 mm ML with rod-like tentacles about the length of arms II; oral surface of tentacle with 4-5 irregular rows of small suckers, only 40-55 in number . . . . . ***Gonatopsis***
   Tentacles present during all life stages; oral surface of tentacle at about <10 mm ML with several rows of minute, very numerous suckers and sucker buds . . . 2
2. Radula with 7 longitudinal rows of teeth . . . . . ***Berryteuthis***
   Radula with 5 longitudinal rows of teeth 3
3. Tentacular club without hooks . . . . . ***Eogonatus***
   Tentacular club with at least one large hook in center . . . . . ***Gonatus***

Key to the North Pacific Species of GONATIDAE (except for *Gonatus ursabrunae, G. oregonensis,* and all *Gonatopsis* except *G. borealis*)

Note: The juveniles and young of the Northwest Pacific species of the family have been studied by Kubodera and Okutani (1981), and the following keys and tables are reproduced from their work.

1. Smaller than about 10 mm ML; tentacular club not developed, oral surface of tentacle equipped with small suckers to the distal tip . . . . . Key-I
   Larger than about 10 mm ML 2
2. Tentacle absent . . . . . ***Gonatopsis borealis*** (11-60 mm ML)
   Tentacle present, tentacular club developed 3
3. Armature of tentacular club not developed, equipped with only numerous minute sucker buds . . . . . Key-II
   Armature of tentacular club developed, equipped with suckers, or suckers and hooks . . . . . Key-III

Key-I (Stage with no tentacular club developed; Table 3a)

1. Mantle wall thin, membranous 2
   Mantle wall muscular, firm to touch 3
2. Mantle bell-shape, base of arms and tentacles tightly constricted making eye protrude, tentacle about 3 times longer than arms . . . . . ***Gonatus madokai*** (8-10 mm ML)
   Mantle swollen spindle-shape with thin epidermis leaving broad space between it and mantle wall, head withdrawn into mantle cavity, tentacle much stouter and longer than arms . ***Gonatus*** sp. type A (6-10 mm ML)
3. Mantle slender cylindrical, MW <40% ML 4
   Mantle squat cylindrical, MW >40% ML 5
4. Radula composed of 5 teeth in transverse row, tentacle armature with 4-5 medial rows of suckers . . . . . ***Gonatus middendorffi*** (6-11 mm ML)
   Radula composed of 7 teeth in transverse row, tentacle armature with 3-4 rows of sparsely beset suckers . . . . . ***Berryteuthis anonychus*** (5-10 mm ML)
5. Tentacle same as arms, tentacle armature with 4-5 rows of sparsely beset suckers . . . . . ***Gonatopsis borealis*** (5-11 mm ML)

TABLE 3a–c.—Morphological comparison of nine gonatid species in early life stages (from Kubodera and Okutani, 1981) (AII = arm II length; ED = eye diameter; FL = fin length; FW = fin width; HW = Head width; ML = mantle length; MO = mantle opening; MW = mantle width; TL = tentacle length; * = ED/ML with photophore).

TABLE 3a.—Stage with no tentacular club developed (smaller than about 10 mm ML).

Species	ML range (mm)	Mantle	MW/ML (%)	Fin	FL/ML (%)	FW/ML (%)	Head	AII/ML (%)	Arm armature	Tentacle	Tentacular armature	Radular teeth
Gonatus onyx	6–10	Bell-shape, muscular	40	Oval	10	45	HW = MO, sometimes withdrawn	25	Suckers and/or buds	TL > AII	5 rows suckers, densely beset	5
Gonatus madokai	8–10	Swollen, bell-shape, soft	35–40	Oval	10–15	35–45	HW < MO, trapezoidal	30	Suckers and/or buds	TL >> AII	4–5 rows suckers, densely beset	5
Gonatus middendorffi	6–11	Slender, bell-shape, muscular	35–40	Oval	10	30	HW = MO	25–30	Suckers and/or buds	TL > AII	4–5 rows suckers, medially beset	5
Gonatus type A	8–10	Swollen, spindle-shape, soft with filmy epidermis	40–45	Oval	10	35	HW = MO, always withdrawn	10–15	Sucker buds	TL >> AII	5–6 rows suckers, densely beset	5
Gonatopsis borealis	5–11	Bell-shape, muscular	40	Oval	10–15	35–45	HW = MO	25–30	Suckers and/or buds	TL = AII	4–5 rows suckers, sparsely beset	7
Berryteuthis magister	7–9	Bell-shape, muscular	40	Oval	10–15	50–60	HW = MO, sometimes withdrawn	40–45	Suckers and/or buds	TL > AII	5–6 rows suckers, densely beset	7
Berryteuthis anonychus	5–10	Slender, bell-shape, muscular	35–40	Oval	15–20	30	HW = MO	40	Suckers and/or buds	TL > AII	3–4 rows suckers, sparsely beset	7

TABLE 3b.—Stage with tentacular club with minute sucker buds.

Species	ML range (mm)	Mantle	MW/ML (%)	Fin	FL/ML (%)	FW/ML (%)	Head	ED/ML (%)	AII/ML (%)	Arm armature	Tentacle	Armature on stalk	Radular teeth
Gonatus berryi	13–22	Elongate, bell-shape, muscular	30–35	Oval to squarish	15	60	HW ≤ MO	24	35–40	Hooks and/or suckers	TL < AII	5–6 rows suckers, densely beset	5
Gonatus onyx	10–15	Bell-shape, muscular	35–40	Oval to squarish	10–25	45–60	HW ≤ MO	20	30–40	Suckers	TL ≥ AII	5 rows suckers, densely beset	5
Gonatus pyros	13.5	Bell-shape, muscular	40	Oval	15	63	HW ≤ MO	20*	38	Suckers	TL > AII	5–6 rows suckers, densely beset	5
Gonatus madokai	10–20	Elongate, bell-shape, soft	30–35	Squarish	15–20	45–60	HW = MO	11–13	30–40	Suckers	TL ≥ AII	4–5 rows suckers, densely beset	5
Gonatus middendorffi	11–35	Slender, cylindrical, muscular	25–40	Squarish to sagittate	10–20	30–40	HW = MO	12–13	30–40	Suckers and/or hooks	TL ≥ AII	4 rows suckers, medially beset	5
Gonatus type A	10–16	Swollen, spindle-shape, soft	40–45	Oval	10–13	35–50	HW = MO, withdrawn	18–20	35–40	Suckers	TL > AII	5–6 rows suckers, densely beset	5
Berryteuthis magister	9–15	Stumpy, bell-shape	35–40	Oval to squarish	20–25	60	HW = MO, sometimes withdrawn	18–20	35–40	Suckers	TL > AII	5–6 rows suckers, densely beset	7
Berryteuthis anonychus	10–25	Slender, cylindrical, muscular	25–35	Oval to squarish	20–25	30–40	HW = MO	15	35–40	Suckers	TL > AII	3–4 rows suckers, sparsely beset	7
Gonatopsis borealis (no tentacles)	>11	Elongate, bell-shape, muscular	30–40	Squarish-sagittate	15–30	45–70	HW = MO	18–20	40	Suckers and/or hooks	–	–	7

TABLE 3c.—Stage with tentacular club developed.

Species	ML range (mm)	Mantle	MW/ML (%)	Fin	FL/ML (%)	FW/ML (%)	Head	ED/ML (%)	AII/ML (%)	Arm armature	Hooks on club	Radular teeth
Gonatus berryi	30	Elongate, bell-shape	30	Sagittate	45	70	HW = MO	22	50	Hooks and/or suckers	2	5
Gonatus onyx	15–26	Elongate, bell-shape	35	Cardioform	25	80	HW = MO	20	55	Hooks and/or suckers	1	5
Gonatus madokai	20–72	Elongate, bell-shape, soft	25–30	Cardioform	20–45	60–90	HW = MO	14–16	60–90	Hooks and/or suckers	2	5
Gonatus middendorffi	35–60	Slender to cylindrical	20–25	Sagittate	20–30	40–50	HW = MO	11–12	45	Hooks and/or suckers	2	5
Gonatus oregonensis	19–46	Plump, widest at middle	29–43	Oval, broad	25–45	80–90	HW < MO	15–23	43–63	Hooks and/or suckers	6	5
Gonatus ursabrunae	12–24	Plump, widest at anterior	30–53	Small	26–50	41–58	HW = MO	18–21	42–56	Hooks and/or suckers	1	5
Berryteuthis magister	16	Stumpy, bell-shape	40	Oval	25	60	HW = MO	18–20	40	Suckers	None	7
Berryteuthis anonychus	25–30	Slender to cylindrical	25	Oval	25	50	HW = MO	13–14	35	Suckers and/or hooks	None	7

Tentacle stouter and longer than arms, tentacle armature with 5–6 rows of densely beset suckers 6

6. Radula composed of 5 teeth in a transverse row . . . . . ***Gonatus onyx*** (6–10 mm ML)
   Radula composed of 7 teeth in a transverse row . . . . . ***Berryteuthis magister*** (7–9 mm ML)

Key-II (Stage with tentacular club with minute sucker buds; Table 3b)

1. Mantle wall thin, soft to touch 2
   Mantle wall thick, muscular, firm to touch 3
2. Mantle elongate bell-shape, MW about 30%–35% ML, eye diameter about 11%–13% ML, arm II about 30%–60% ML . . ***Gonatus madokai*** (10–20 mm ML)
   Mantle spindle-shape with thin epidermis, MW about 40%–45% ML, eye diameter about 15%–17% ML, arm length not exceeding 30% ML . . . . . ***Gonatus*** sp. type A (10–16 mm ML)
3. Large oval photophore on ventral surface of both eyes . . . . . ***Gonatus pyros*** (13.5 mm ML)
   No photophore on eye 4
4. Median 2 rows of Arms I, II, and III developed into hooks . . . . . ***Gonatus berryi*** (13–22 mm ML)
   Median 2 rows of Arms I, II, and III not yet developed into hooks 5
5. Mantle long, slender, cylindrical, MW about 25%–35% ML 6
   Mantle bell-shape, MW about 35%–40% ML 7
6. Medial 4 rows of suckers densely beset in proximal portion of immature club, radula composed of 5 teeth in transverse row . . . . . ***Gonatus middendorffi*** (11–35 mm ML)
   Irregular 3–4 rows of suckers sparsely beset in proximal portion of immature club, radula composed of 7 teeth in transverse row . . . . . ***Berryteuthis anonychus*** (10–30 mm ML)
7. Radula composed of 5 teeth in transverse row, proximal portion of immature club with 5 rows of densely beset suckers . . . . . ***Gonatus onyx*** (10–15 mm ML)
   Radula composed of 7 teeth in transverse row, proximal portion of immature club with 5–6 rows of densely beset suckers . . . . . ***Berryteuthis magister*** (9–15 mm ML)

Key-III (Stage with developed tentacular club; Table 3c)

1. Tentacular club with immature hook 2
   Tentacular club with no hook, only suckers 5
2. Mantle wall thin, not so muscular, soft, MW about 25%–30% ML, arm length 60%–90% ML . . . . . ***Gonatus madokai*** (20–72 mm ML)
   Mantle wall thick, muscular 3
3. Mantle long slender, MW about 20%–25% ML . . . . . ***Gonatus middendorffi*** (35–60 mm ML)
   Mantle elongated-bell, MW about 30%–35% ML . . . 4
4. Tentacular club with single large central hook without additional hook . . . . ***Gonatus onyx*** (15–26 mm ML)
   Small additional hook present distal to large central hook, central hook situated at extreme distal portion of manus . . . . . ***Gonatus berryi*** (30 mm ML)
5. Mantle slender cylindrical, MW about 23%–25% ML, small fins about half of ML in width . . . . . ***Berryteuthis anonychus*** (25–30 mm ML)
   Mantle squat, MW about 40% ML, large fins about 60% ML in width . . . ***Berryteuthis magister*** (16 mm ML)

Gonatus Gray, 1849

GENERIC CHARACTERS.—Tentacular club with large central hook and generally additional hooks in median line; club with distinctive locking-apparatus on dorsal border of manus that consists of a series of large, thick, transverse pads with medial alternating oval pads and suckers; radula with 5 rows of teeth.

Gonatus fabricii (Lichtenstein, 1818)

SPECIES CHARACTERS.—*Adults* (Figure 185): 37–52 suckers/hooks on proximal half of arms III; 57–69 suckers (no hooks) on proximal half of arms IV; tentacles long, slender with small clubs, 12%–20% gladius length (GL); club with 1 large central hook and 3 smaller hooks and 1 sucker distally; 2 large chromatophores on ventral surface of head; ventral pads of funnel organ about 50% length of each ramus of dorsal pad; radula with smooth lateral teeth, no ridges.

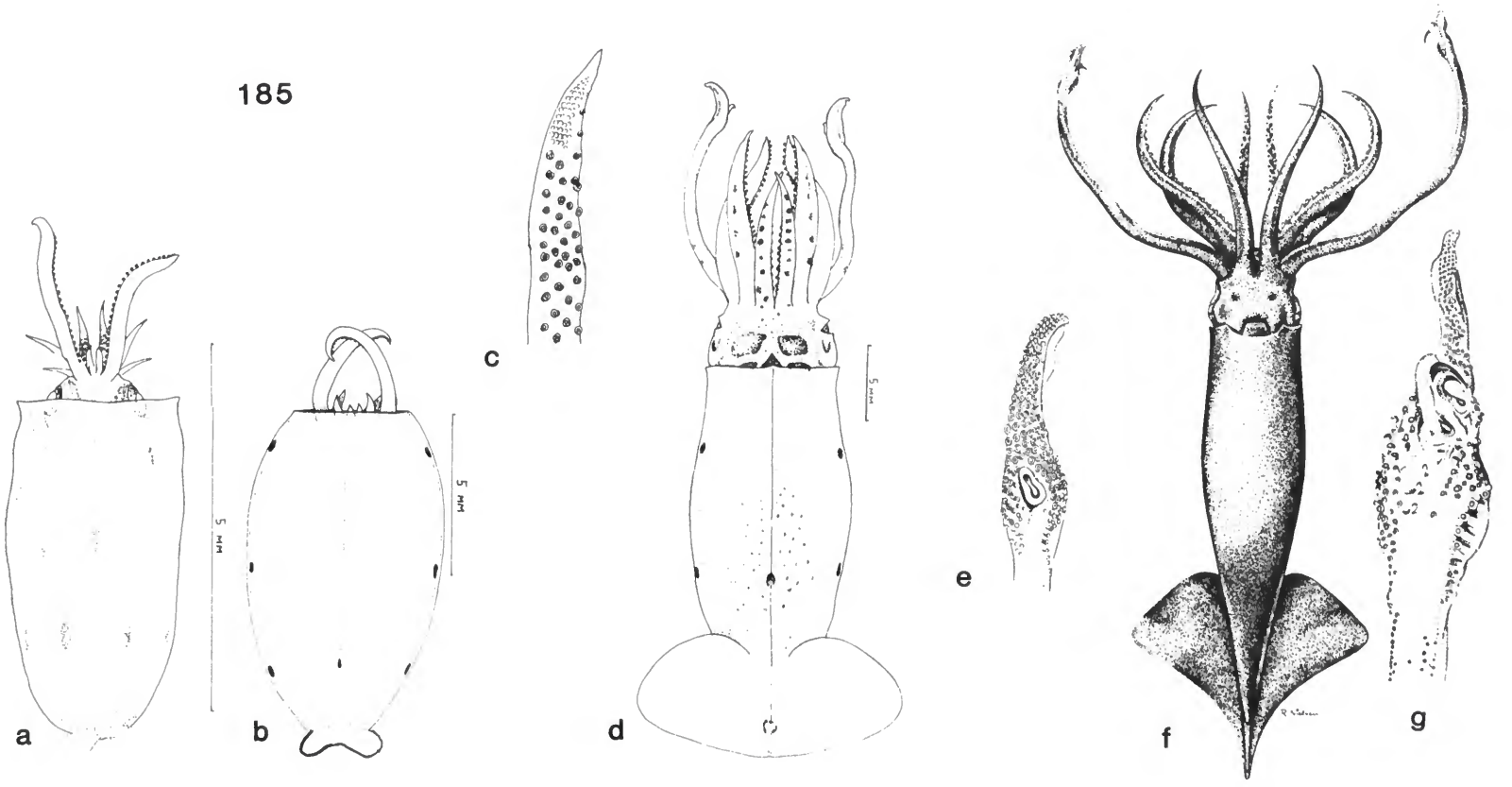
GEOGRAPHICAL DISTRIBUTION.—Arctic waters north of about 60°N but extends south to 46°N on western side of Atlantic.

Gonatus antarcticus Lonnberg, 1898

SPECIES CHARACTERS.—*Adults:* Small marginal suckers on arms I–III relative to arm IV; tentacular stalk with numerous suckers (118–190); tentacular club small, with large number of suckers (270), 3–4 hooks proximal to central large hook, hooks decrease in size proximally; fin narrow, FWI ~50°.

Young (Figure 186): 27 mm ML juvenile from Chile-Peru Current; hooks on arms; central and distal hooks (but not proximal hooks) on tentacular club fully developed; tentacular club similar to *G. californiensis*, but arms somewhat longer, number of suckers and hooks higher in *antarcticus* (Nesis, 1973).

GEOGRAPHICAL DISTRIBUTION.—Southern Ocean south of 40°S, probably circumpolar (Clarke, 1980; Kubodera and Okutani, 1986); may extend as far north as about 6°S in the Chile-Peru Current.



FIGURES 185.—*Gonatus fabricii* (*a–e*, North Pacific; *f,g*, North Atlantic): *a,b*, and *d*, dorsal view of growth series; *c* and *e*, tentacular club of *b* and *d*, respectively (*a–e*, from Okutani, 1966); *f*, ventral view of neotype, 129 mm GL, North Atlantic; *g*, tentacular club of *f* (*f,g*, from Kristensen, 1981).

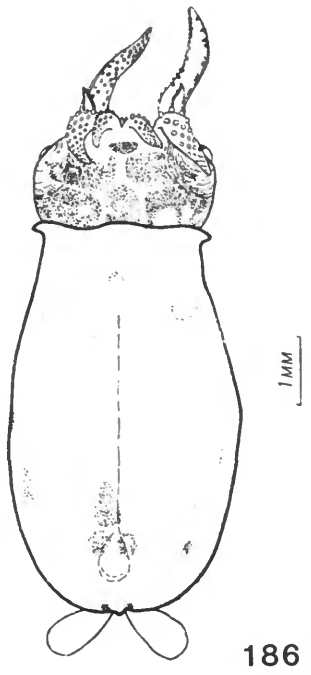


FIGURE 186.—*Gonatus antarcticus*, dorsal view, 5.7 mm ML, Chile-Peru Current. (From Nesis, 1973.)

Gonatus berryi Naef, 1923

SPECIES CHARACTERS.—*Adults:* 25–33 suckers/hooks on proximal half of arms III; 40–50 suckers (no hooks) on proximal half of arms IV; tentacles robust, 30%–37% GL, stalk without suckers between marginal rows; median zone of tentacular club with 1–2 suckers near large central tooth, several other hooks decrease in size distally from large central tooth; ventral-marginal portion of club with 2 marginal rows of large suckers plus 1–2 rows of minute suckers medially; dactylus with ventral rows of suckers smaller than dorsal row.

Young (Figure 187*a–d*): Hooks develop on arms at 8–10 mm GL; spindle-shape larval liver absent from life cycle; mantle elongate bell-shape, MW = 30%–33% ML; arm formula II, III, I, IV; hooks present in median two rows by 13 mm ML on center of arm I–III, arm hooks present prior to club hooks; CL = 25% (30 mm ML) to10% (13 mm ML).

GEOGRAPHICAL DISTRIBUTION.—North Pacific, 30°N (eastern) to 40°N (central) to approximately 37°N (western).

Gonatus californiensis Young, 1972

SPECIES CHARACTERS.—*Adults* (Figure 188): Mantle long, slender; tentacular club small, 17%–24% GL, median zone with very large central hook with (distally) moderately large hook and (proximately) 3–5 small hooks; tentacular stalk with numerous suckers between marginal rows; arm IV sucker count constant at 60–65 mm ML.

GEOGRAPHICAL DISTRIBUTION.—Eastern Pacific 28°N to about 50°N.

Gonatus madokai Kubodera and Okutani, 1977

SPECIES CHARACTERS.—*Adults:* Arms long (AIII/ML = 90.9%); tail long (20% ML); body soft; fins large, about 50% ML; thin membranous aboral keels on arm III and IV; manus of club with large central hook plus one distal hook.

Young (Figure 189*g–l*): Mantle soft, elongate bell-shape in larger specimens, swollen bell-shape in smaller specimens; eye diameter large (16% ML); arm formula III, II, IV, I in larger specimens, III, II, I, IV in smaller specimens; median 2 rows of arms I–III change to hooks at 20–30 mm ML; tentacles stout, longer than arms (<15 mm ML).

GEOGRAPHICAL DISTRIBUTION.—North Pacific around Kamchatka, southern limits of 42°N (eastern), 45°N (central), and 42°N (western) to ~58°N.

Gonatus middendorfii Kubodera and Okutani, 1981

SPECIES CHARACTERS.—*Adults* (Figure 187*i,j*): Mantle long, slender (MW = 18% ML); arms short (AIII = 50% ML); body muscular; tentacles weak with small clubs (CL = 12% ML); manus with large central hook, 1 distal hook, 5–6 small proximal suckers (2–3 sometimes modified into small hooks).

Young (Figure 187*e–h*): Mantle long, slender, muscular; tentacular club with 2 hooks on manus (>30 mm ML), median 4 rows of small suckers proximal to immature club (11–30 mm ML); arm formula II, III, I, IV.

GEOGRAPHICAL DISTRIBUTION.—Western Pacific (42°N to 62°N) to southern side of Aleutian Island chain (140°W).

Gonatus onyx Young, 1972

SPECIES CHARACTERS.—*Adults:* Arms I smallest, 40%–50% GL, arms II, III muscular, 50%–60% GL; 25–30 suckers on proximal half of arms I–III; tentacles robust with small, complex clubs (20%–25% GL); clubs generally with single hook (occasionally enlarged distal sucker), proximal suckers never transformed into hooks; tentacular stalk suckers between marginal rows usually <10.

Young (Figure 189*a–f*) Mantle elongate bell-shape; arms stout, muscular; arm formula II, III, IV, I or II, III, I, IV (<20 mm ML); median rows of arms I–III change to hooks at 18–20 mm ML; median zone of manus with large immature hook (13–15 mm ML) with 2–4 small proximal suckers and no large sucker bud or immature hook on distal side, club with only minute sucker buds with distinct immature central hook (<12–13 mm ML).

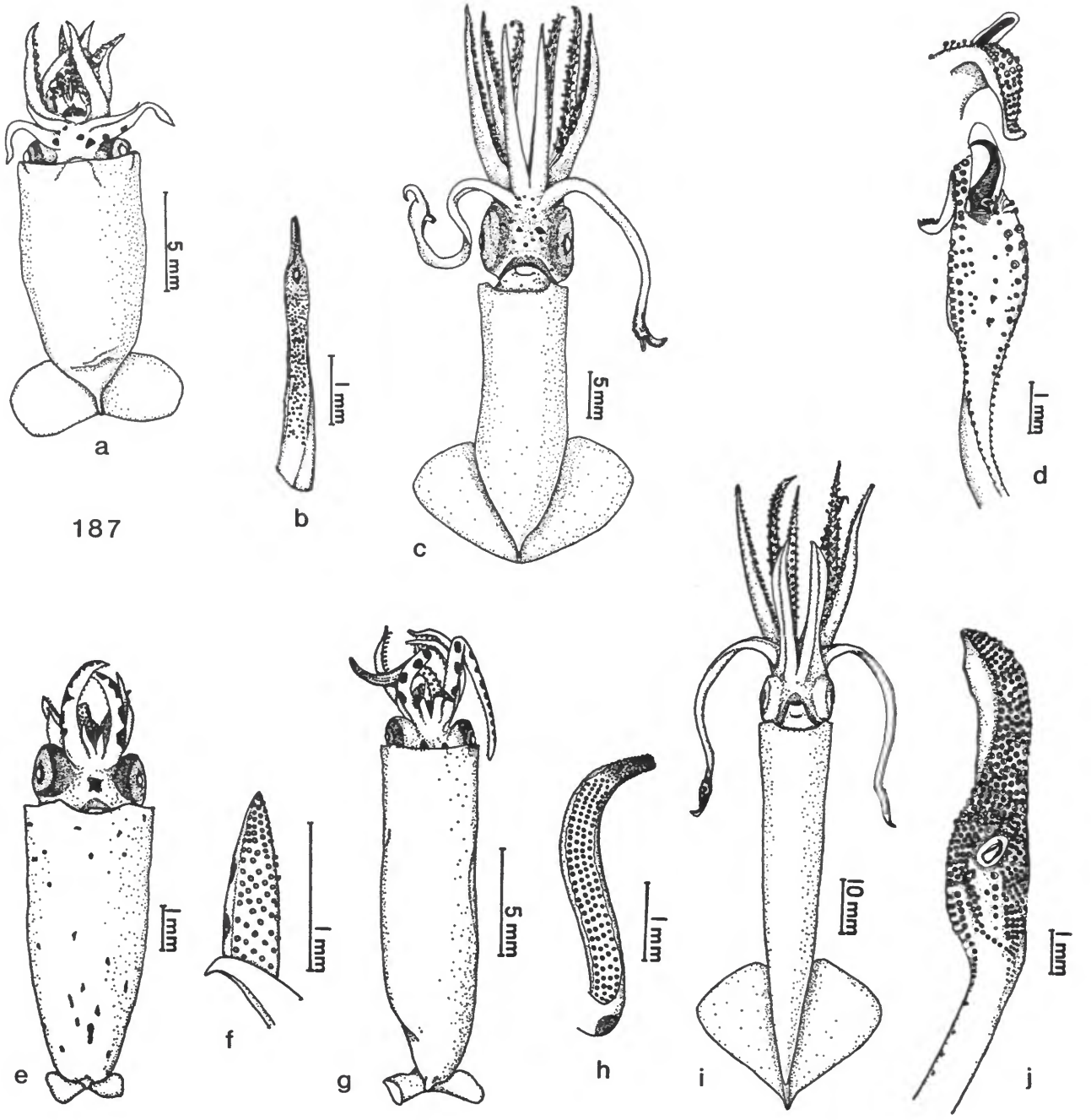


FIGURE 187.—*a–d, Gonatus berryi,* ventral view and tentacle: *a,b,* 13 mm ML specimen; *c,d,* 30 mm ML specimen. *e–j, Gonatus middendorffi,* ventral view and tentacle: *e, f,* 6.3 mm ML specimen; *g,h,* 16 mm ML specimen; *i,j,* 72 mm ML specimen. (From Kubodera and Okutani, 1981.)

FIGURE 188.—*Gonatus californiensis*, northeastern Pacific, holotype: *a*, ventral view, 112 mm GL; *b*, tentacular club of same. (From Young, 1972.)

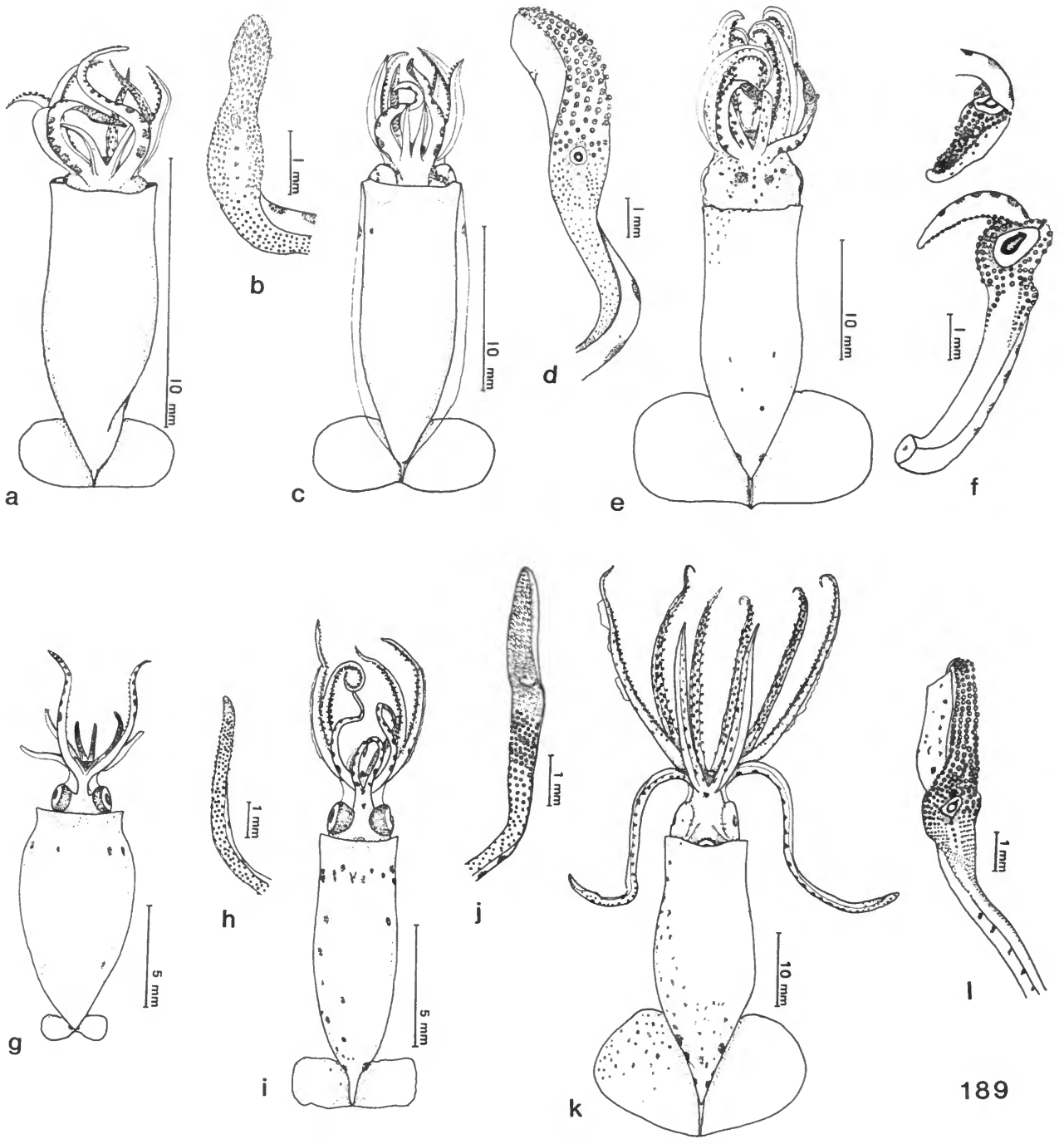


FIGURE 189.—*a–f, Gonatus onyx,* ventral view and tentacle, North Pacific: *a,b,* 11 mm ML; *c,d,* 22 mm ML; *e, f,* 40 mm ML. *g–l, Gonatus madokai,* ventral view and tentacle, North Pacific: *g,h,* 11 mm ML; *i,j,* 18 mm ML; *k,l,* 26 mm ML. (From Kubodera and Okutani, 1981.)

GEOGRAPHICAL DISTRIBUTION.—North Pacific from 30°N (eastern), 42°N (central), 35°N (western) to Bering Sea.

Gonatus oregonensis Jefferts, 1985

SPECIES CHARACTERS.—*Young* (Figure 190): Club with 295–370 dactylus suckers arranged in 7–8 rows at base decreasing to 5–6 rows near tip; arm II 50%–67% ML at 29–46 mm ML.

GEOGRAPHICAL DISTRIBUTION.—North Pacific; off Oregon.

REMARKS.—Largest specimen is a 46 mm ML juvenile. *G. oregonensis* can be separated from most *Gonatus* species by the distribution of tentacular hooks. However, *G. oregonensis* is separable from *G. californiensis* only in body proportions such as, FWI (80–89 in *oregonensis* versus 54–70 in *californiensis*), CLI (21–30 versus 17–24) and club sucker counts (295–370 versus 217–269).

Gonatus pyros Young, 1972

SPECIES CHARACTERS.—*Adults* (Figure 191*a,b*): Head short, round; eyes large with single, large, white photophore on ventral surface; tentacles long, robust; tentacular club short, expanded, very complex, CL = 20%–25% GL; tentacular

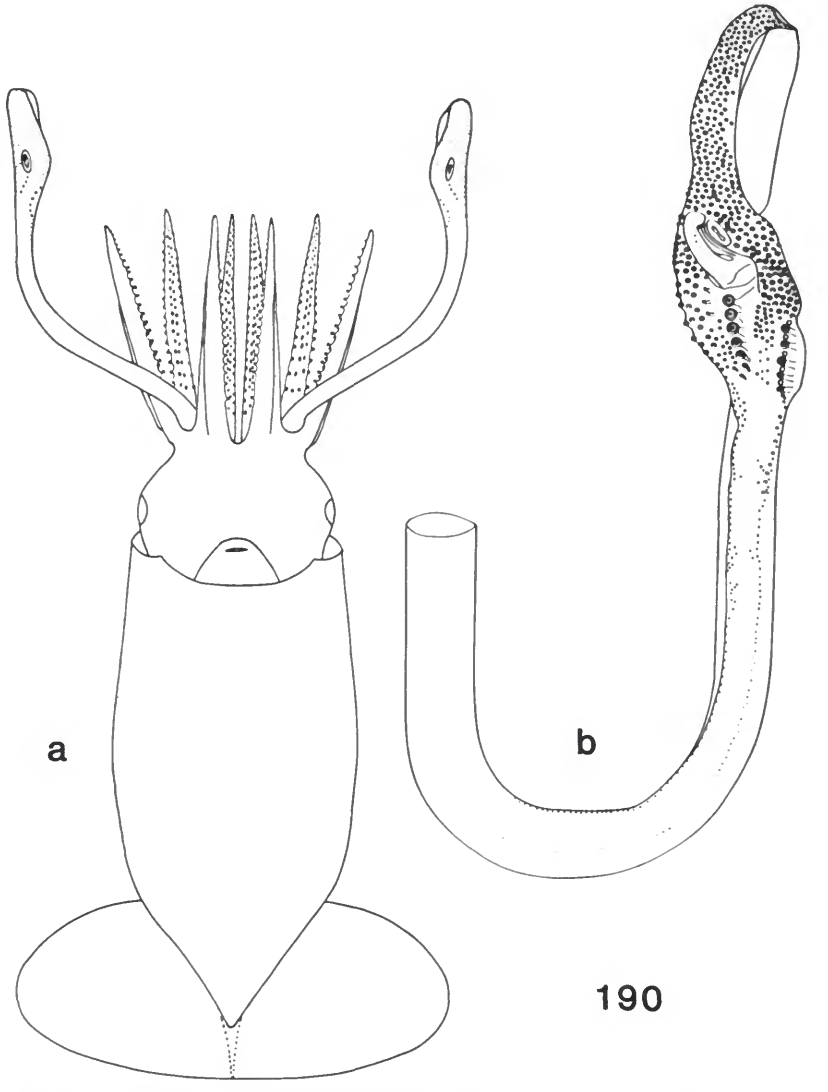


FIGURE 190.—*Gonatus oregonensis*, northeastern Pacific, paratype: *a*, ventral view, 46 mm ML; *b*, tentacular club of same. (From Jefferts, 1985.)

stalk with double row of suckers on ventral margin.

Young (Figure 191*c,d*): Mantle elongate bell-shape, thin, muscular; head slightly smaller than mantle opening; large eyes with large, oval, ventral patch of photogenic tissue; arm formula II, III, I, IV.

GEOGRAPHICAL DISTRIBUTION.—Northern and eastern Pacific, 32°N (eastern), 42°N (western) to Bering Sea.

Gonatus steenstrupi Kristensen, 1981

SPECIES CHARACTERS.—*Adults* (Figure 192): 31–42 suckers/hooks on proximal half of arms III; 46–57 suckers (no hooks) on proximal half of arms IV; tentacles strong and moderately long with large clubs 20%–36% GL; club with 1 large central hook and 4–5 smaller hooks and sometimes 1

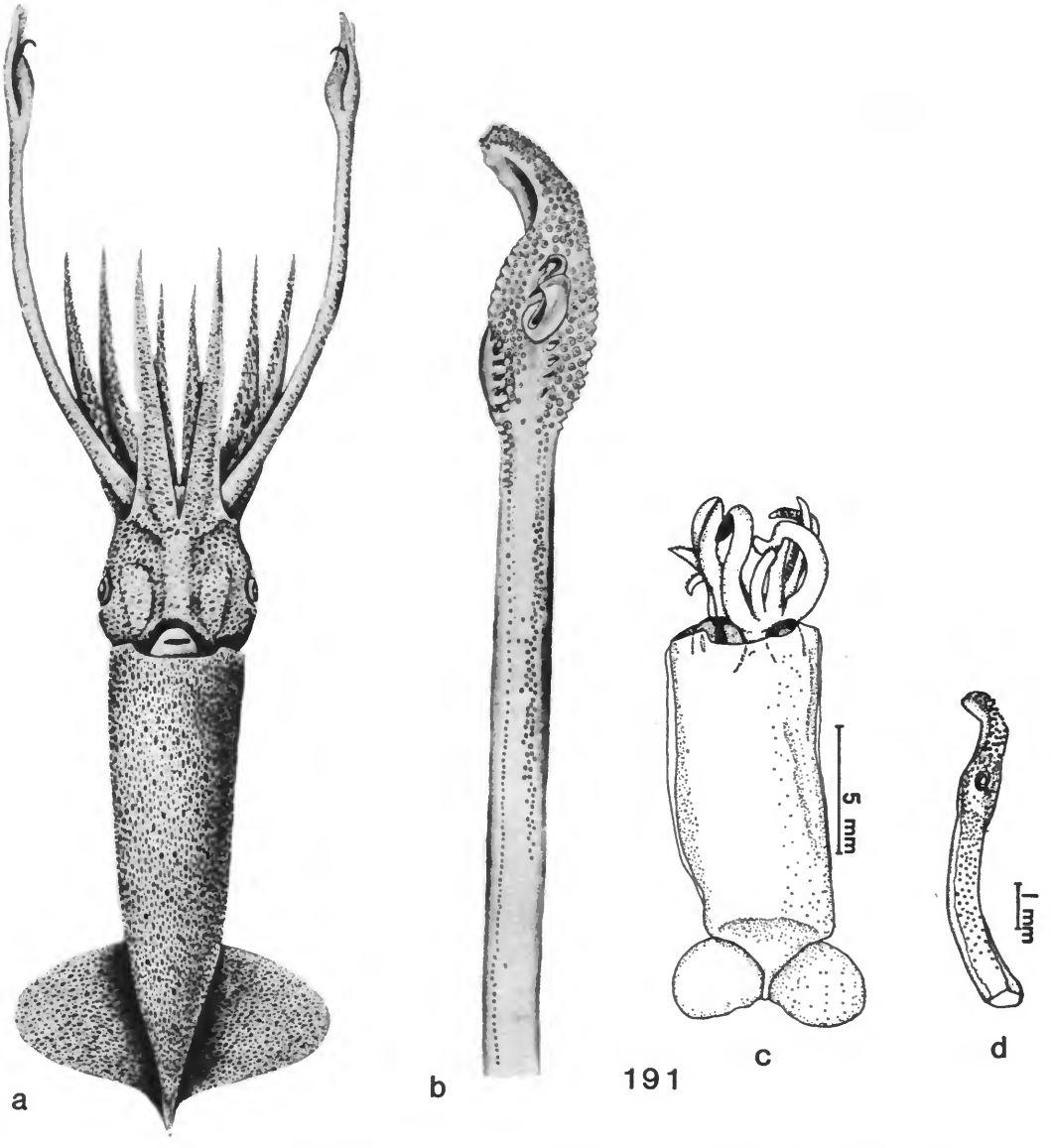


FIGURE 191.—*Gonatus pyros*, northeastern Pacific: *a*, ventral view, 39 mm ML; *b*, tentacle of 35? mm ML specimen (both from Young, 1972); *c*, ventral view, 13.5 mm ML; *d*, tentacle of same (both from Kubodera and Okutani, 1981).

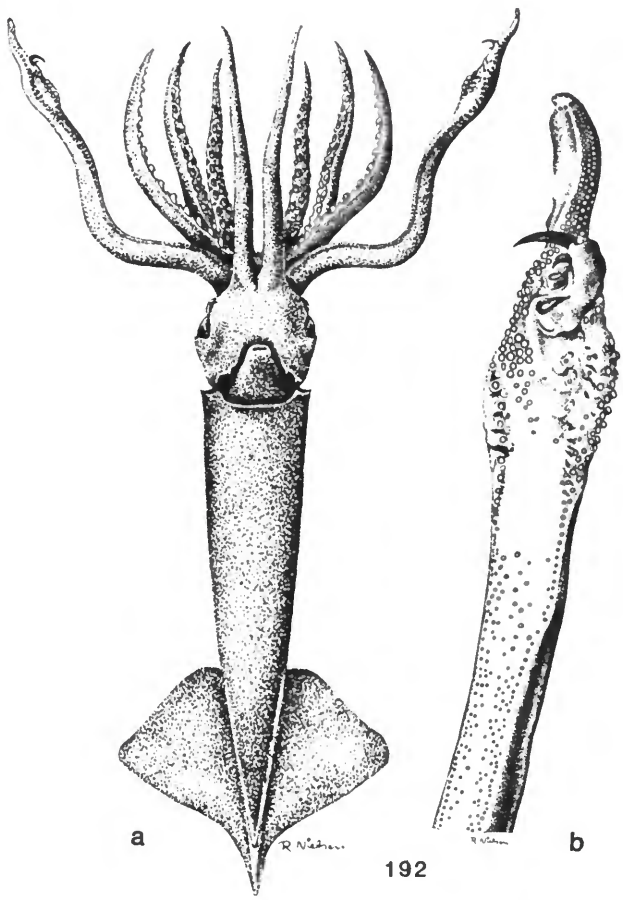


FIGURE 192.—*Gonatus steenstrupi*, North Atlantic, holotype: *a*, ventral view, 94 mm ML; *b*, tentacular club of same. (From Kristensen, 1981.)

sucker distally; ventral pads of funnel organ about 66% length of each ramus of dorsal pad; radula with lateral teeth profiled by a ridge.

GEOGRAPHICAL DISTRIBUTION.—North Atlantic 45°N to 63°N; Mediterranean?

Gonatus ursabrunae Jefferts, 1985

SPECIES CHARACTERS.—*Young* (Figure 193): Lateral suckers of middle portions of arms I-III and proximal portion of dactylus are greatly enlarged; tentacular club with approximately 110 suckers distal to tentacle hook.

GEOGRAPHICAL DISTRIBUTION.—North Pacific; Oregon to central Aleutian Islands.

REMARKS.—Largest specimen known is a 24 mm ML juvenile.

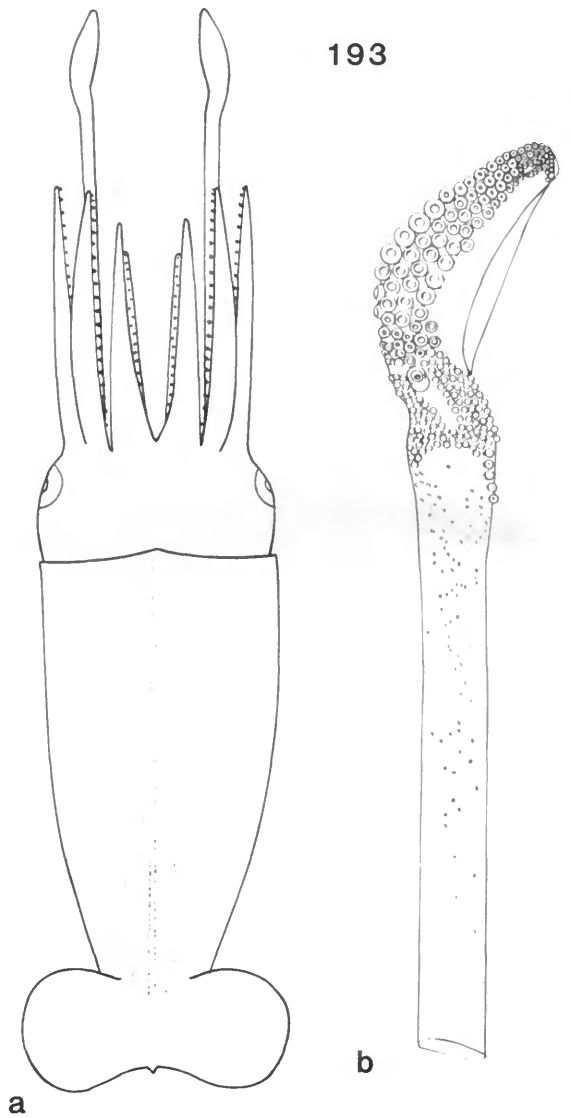


FIGURE 193.—*Gonatus ursabrunae*, northeastern Pacific, paratype: *a*, dorsal view, 19 mm ML; *b*, tentacular club of same. (From Jefferts, 1985.)

Eogonatus Nesis, 1972

GENERIC CHARACTERS.—*Adults* (Figure 194*a,b*): Tentacles very weak, without hooks, but with very crowded small suckers; fins rather round, not sagittate as in other gonatids.

Young: See Figure 194*c,d*.

REMARKS.—No further discussion is presented in the absence of study material of *E. tinro*. Illustrations are shown from the original description (Figure 194).

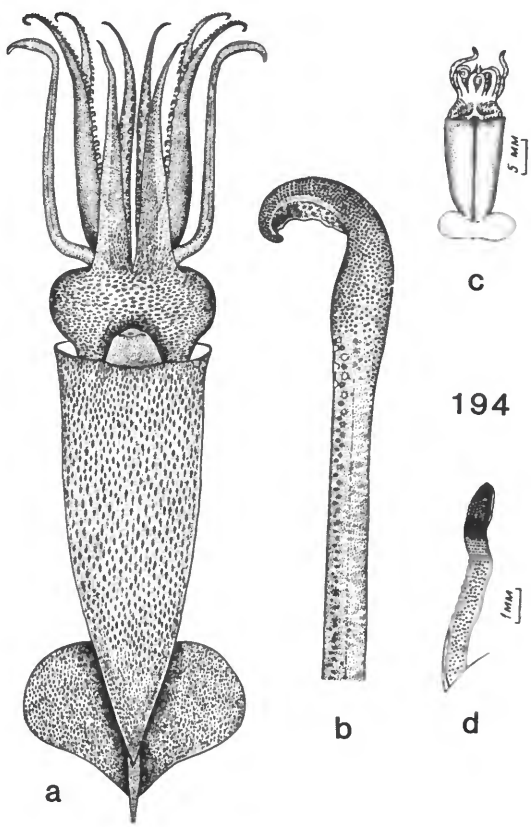


FIGURE 194.—*Eogonatus tinro*, North Pacific: *a*, ventral view; *b*, tentacle of same; *c*, dorsal view, 17.5 mm ML; *d*, tentacle of 15.5 mm ML specimen. (From Nesis, 1972.)

Gonatopsis Sasaki, 1920

GENERIC CHARACTERS.—*Adults:* No tentacles, except in *G. okutani* at <11 mm ML, with 4–5 rows of suckers; radula with 5 or 7 rows of teeth.

REMARKS.—Nesis (1971) separated this genus into two subgenera; *Boreoteuthis* with 7 longitudinal rows of teeth (*G. borealis*) and *Gonatopsis s.s.* with 5 longitudinal rows of teeth (all other *Gonatopsis* species).

Gonatopsis octopedatus Sasaki, 1920

SPECIES CHARACTERS.—*Adults:* Arms I–III with 8–12 longitudinal rows of suckers.

GEOGRAPHICAL DISTRIBUTION.—Sea of Okhotsk, Northwest Pacific, and North Japan Sea.

REMARKS.—Poorly known; see description in Okiyama (1970).

Gonatopsis borealis Sasaki, 1923

SPECIES CHARACTERS.—*Adults* (Figure 195*a*): Mantle stout, thick, muscular; fin length 40%–45% ML; fin width 65%–70% ML; tentacles present only in larva; arms 40%–50% ML; arms I–III with median hooks and marginal suckers.

Young (Figure 195*b–f*): Mantle elongate bell-shape; MW 30%–40% ML; fins oval; eyes large, 18%–20% ML; arms thick, stout, arm formula II, III, I, IV; 4 rows of armature on arms I–III with median 2 rows of suckers changing to hooks at 30–35 mm ML; tentacles absent at >10–12 mm ML.

GEOGRAPHICAL DISTRIBUTION.—North Pacific from Japan (37°N) through a portion of Bering Sea (Murata and Okutani, 1975) to California (33°N).

Gonatopsis japonicus Okiyama, 1969

SPECIES CHARACTERS.—*Young* (Figure 196): Fin sagittate with acute posterior end, length 53% ML, width 50% ML; longest arm length 57% ML; head exceeds mantle in width; radula with 5 rows of teeth.

GEOGRAPHICAL DISTRIBUTION.—Japan Sea (possibly farther north).

REMARKS.—This species may represent an immature stage of *Gonatopsis makko*.

Gonatopsis makko Okutani and Nemoto, 1964

SPECIES CHARACTERS.—*Adults:* Mantle long, slender; fins small, length 33% ML, width 45%–50% ML; arms long, 80% ML.

GEOGRAPHICAL DISTRIBUTION.—North Pacific from Japan to Alaska; not found in open ocean.

REMARKS.—This species may represent the adult of *Gonatopsis japonicus*.

Gonatopsis okutanii Nesis, 1972

SPECIES CHARACTERS.—*Adults* (Figure 197): Body soft, almost gelatinous; rudiments of tentacles even in adult; arms very long (≥100% ML).

GEOGRAPHICAL DISTRIBUTION.—Northwest Pacific, Japan Sea to western Bering Sea.

Berryteuthis Naef, 1923

GENERIC CHARACTERS.—*Young* (Figure 198): Tentacles with very crowded suckers only; club with fixing apparatus consisting of suckers and knobs, without alternating transverse

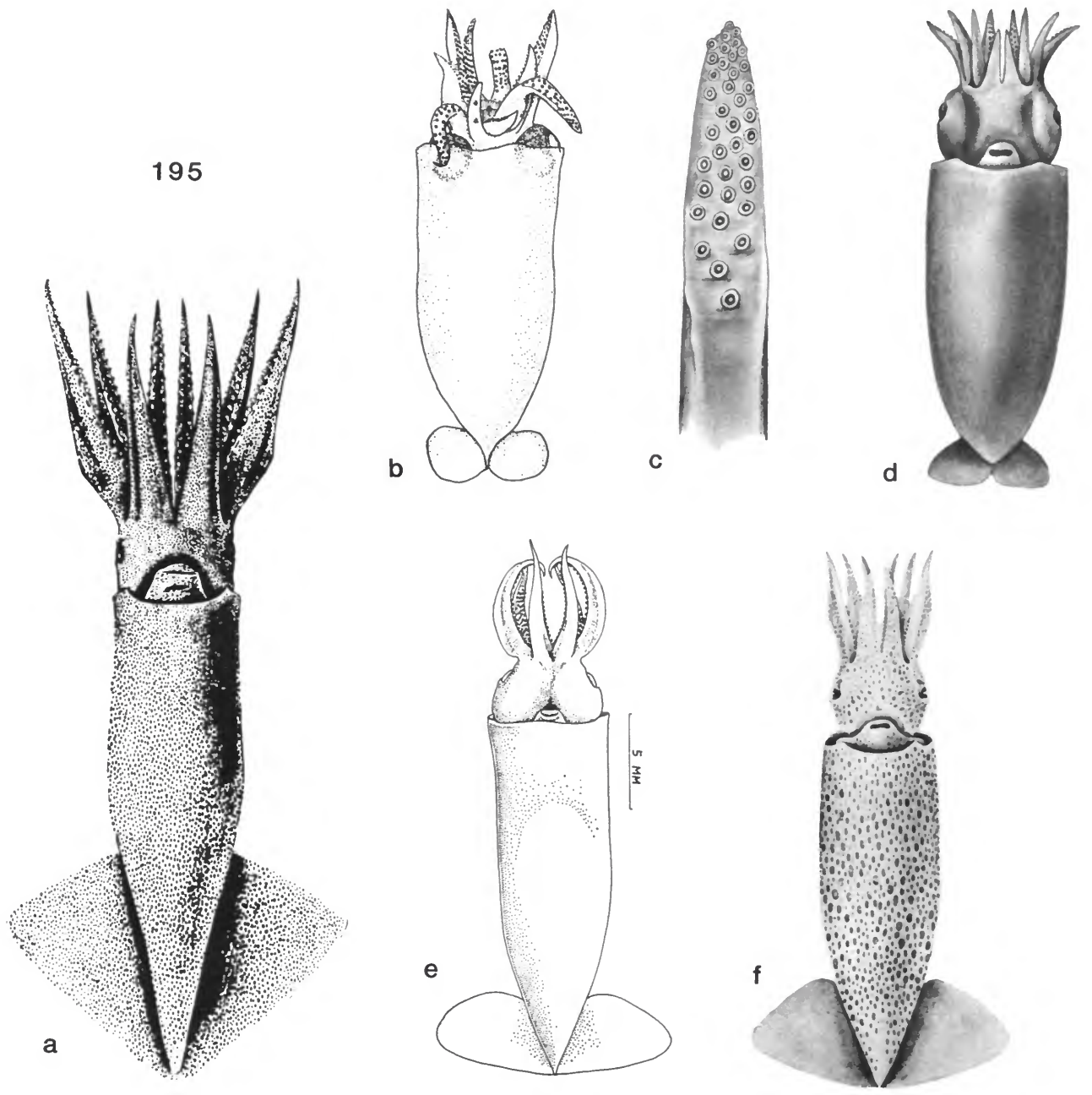
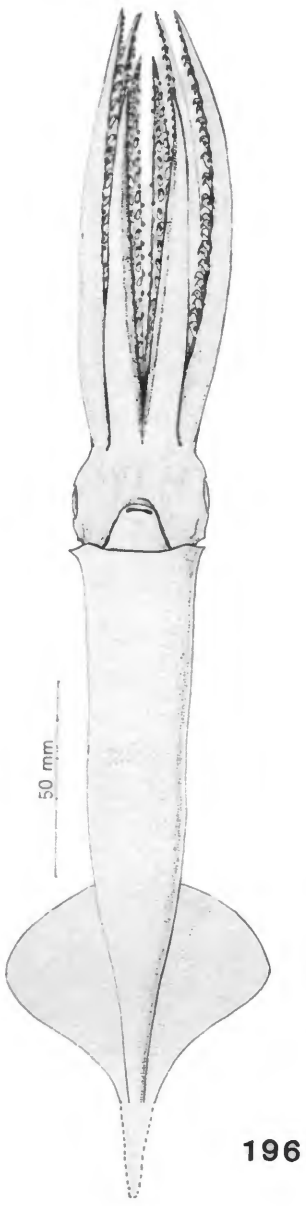


FIGURE 195.—*Gonatopsis borealis*, ventral views: *a*, northeastern Pacific, 240 mm ML (from Young, 1972); *b*, North Pacific, 7.5 mm ML (from Kubodera and Okutani, 1981); *c*, northeastern Pacific, tentacle of 7.0 mm ML specimen; *d*, northeastern Pacific, 9.0 mm ML (both from Young, 1972); *e*, North Pacific, ~20 mm ML (from Okutani, 1966); *f*, northeastern Pacific, 35 mm ML (from Young, 1972).



FIGURES 196.—*Gonatopsis japonicus*, ventral view, 150+ mm ML, northwestern Pacific. (From Murata and Okutani, 1975.)

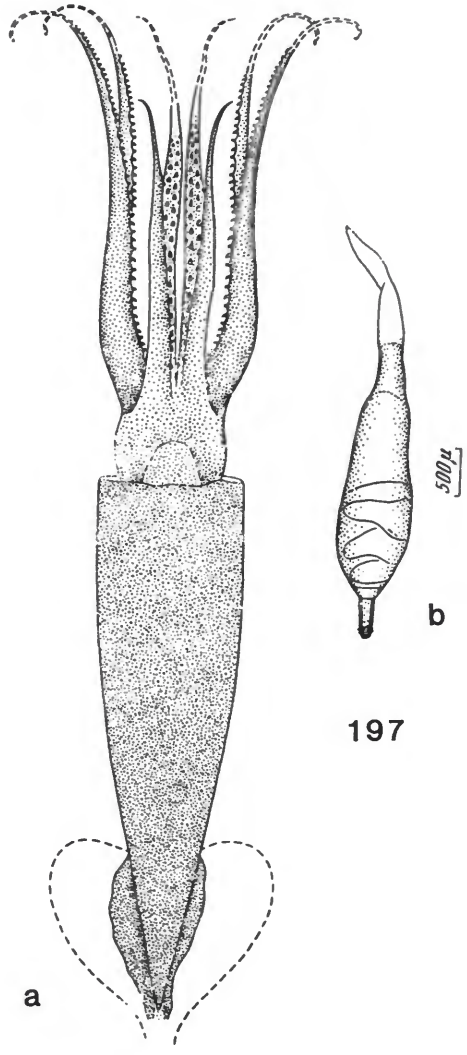


FIGURE 197.—*Gonatopsis okutani: a*, ventral view, North Pacific; *b*, egg. (From Nesis, 1972.)

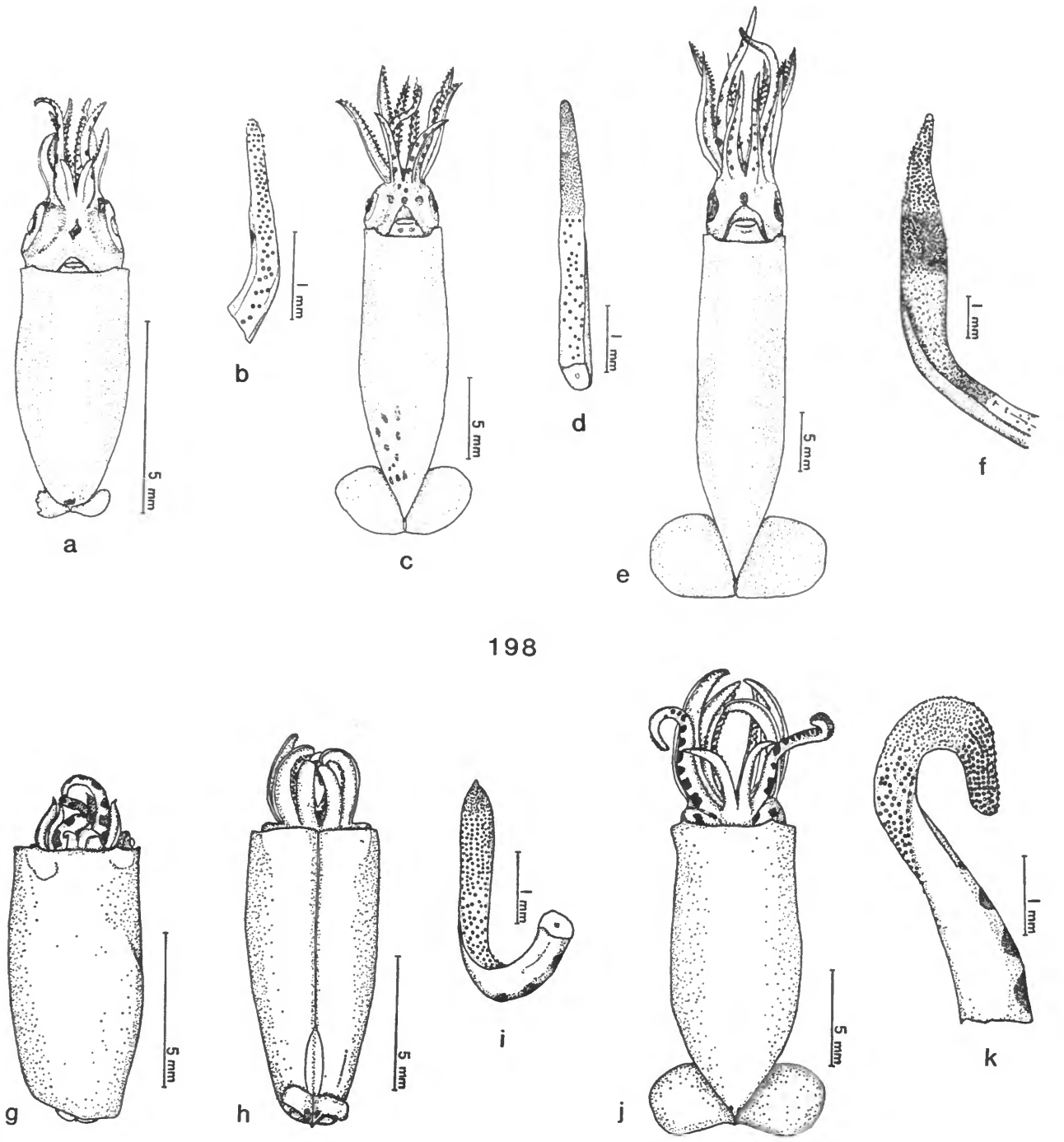


FIGURE 198.—*a–f, Berryteuthis anonychus*, ventral view and tentacle, North Pacific: *a,b,* 6 mm ML; *c,d,* 23 mm ML; *e, f,* 30 mm ML. *g–k, Berryteuthis magister*, ventral view and tentacle, North Pacific: *g,* 9 mm ML; *h,i,* dorsal view, 12 mm ML; *j,k,* 16 mm ML. (From Kubodera and Okutani, 1981.)

ridge and groove; hooks on arms present in small numbers or absent; radula with 7 transverse rows.

Berryteuthis anonychus (Pearcy and Voss, 1963)

SPECIES CHARACTERS.—*Young* (Figure 198*a–f*): Mantle cylindrical, slender, muscular; fins nearly oval; head cylindrical, usually not withdrawn in mantle cavity; eye diameter 13%–16% ML; arms short, slender; arm formula II, I, III, IV.

GEOGRAPHICAL DISTRIBUTION.—Northeastern Pacific.

Berryteuthis magister (Berry, 1913)

SPECIES CHARACTERS.—*Young* (Figure 198*g–k*): Mantle stumpy, bell-shape, thin, muscular; fins small; head large almost ovoid, generally withdrawn into mantle cavity; eye diameter 20%–25% ML; arms thick, stout; arm formula II, III, I, IV.

GEOGRAPHICAL DISTRIBUTION.—Pansubarctic Pacific.

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Family BRACHIOTEUTHIDAE Pfeffer, 1908

(by C.F.E. Roper and M.J. Sweeney)

FAMILY CHARACTERS.—*Adults:* Elongate, posteriorly pointed mantle; broad, lanceolate fins; numerous rows of small suckers on proximal portion of tentacular club; distinct oval suckered tip of dactylus; alternating rows of suckers and pads along tentacular stalk; simple straight funnel locking-cartilage; buccal connectives attach to ventral borders of arms IV; 2 rows of suckers on arms; ocular photophores present in some species. Monogeneric.

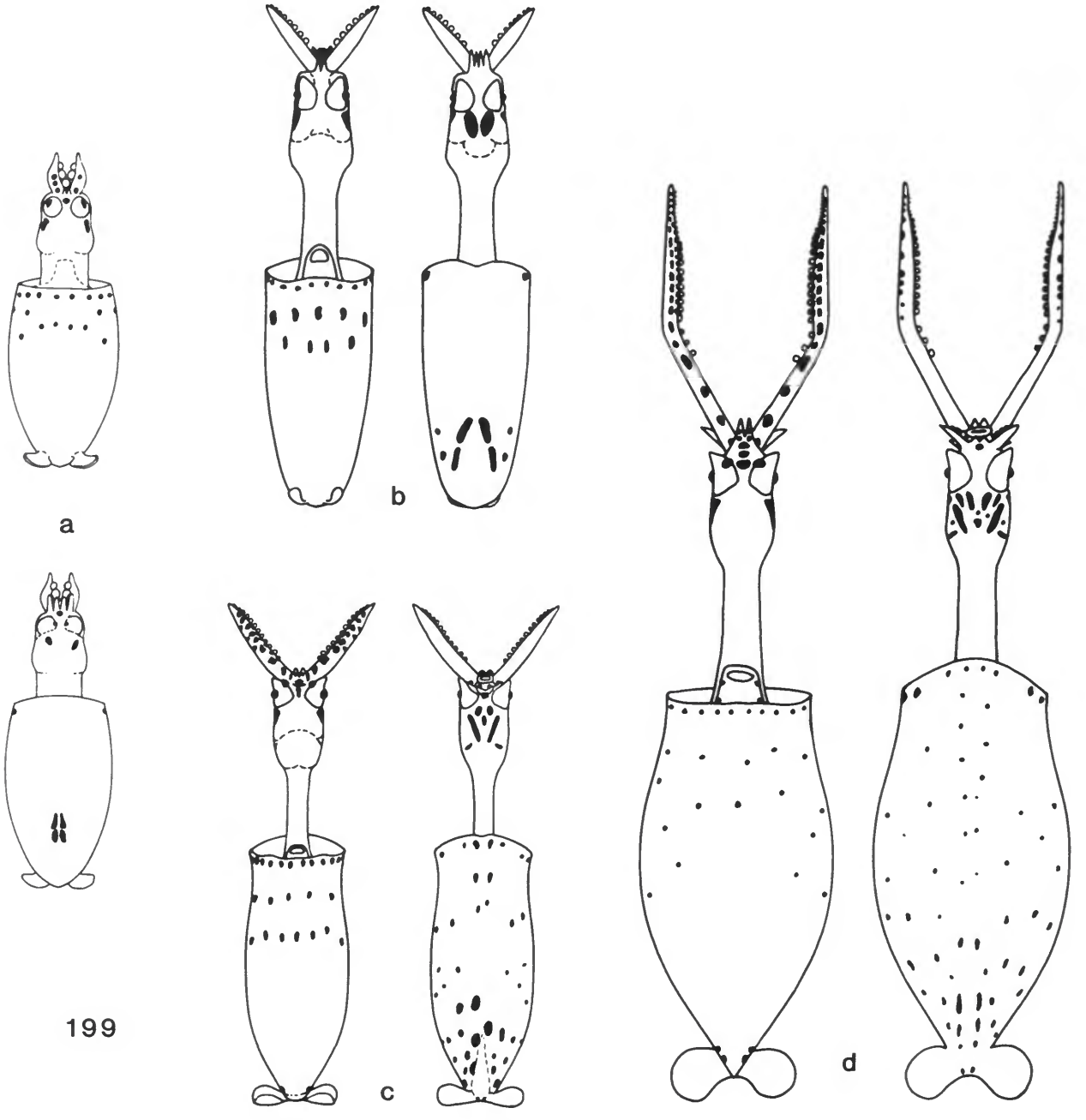

FIGURE 199.—*Brachioteuthis* sp., ventral and dorsal views, Hawaiian waters: *a*, 2.0 mm ML, 5 days after hatching; *b*, 2.6 mm ML; *c*, 5.4 mm ML; *d*, 9.1 mm ML. (From Young et al., 1985.)

Brachioteuthis Verrill, 1881

GENERIC CHARACTERS.—*Young* (Figures 199, 200): Mantle elongate to elongate/bulbous; fins separate, terminal, paddle-shape, transversely oval; distinctive long, slender neck (no arm-crown stalk); eyes lateral but frequently occur toward ventral part of head; distinctive swelling on dorsal surface of head; mantle opening wide relative to neck; club suckers develop at hatching and adult-like pattern of numerous suckers on proximal manus well established by about 10 mm ML; tentacles large, present at hatching, robust relative to arms.

Eggs: Elongate, 1.2 × 0.73 mm, without pronounced perivitelline spaces; chorion lacks obvious ornamentation; occur singly (*Brachioteuthis* sp., Hawaii, Young et al., 1985).

GEOGRAPHICAL DISTRIBUTION.—Found in all oceans.

VERTICAL DISTRIBUTION.—*Brachioteuthis* is suspected of undergoing extensive diel vertical migrations (Roper and Young, 1975) but more closing-net material is needed for confirmation. Zuev and Nesis (1971) report young in surface layers (0–100 m), larger individuals in intermediate layers, and some captures to 2000–3000 m. Clarke and Lu (1974) report a few young and juveniles (8–35 mm ML) between 0 and 200 m

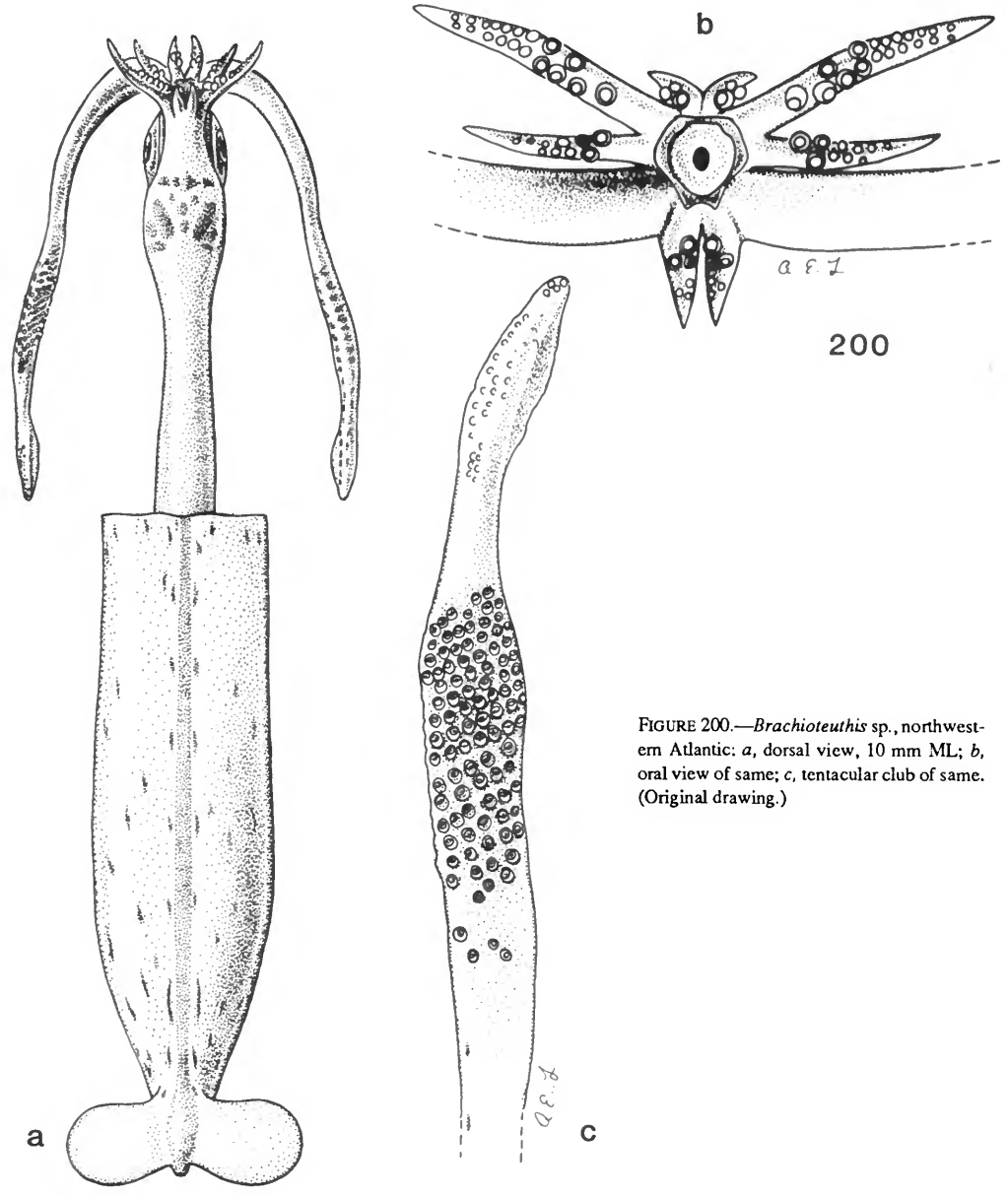

FIGURE 200.—*Brachioteuthis* sp., northwestern Atlantic: *a*, dorsal view, 10 mm ML; *b*, oral view of same; *c*, tentacular club of same. (Original drawing.)

and Lu and Clarke (1975) demonstrated that "larvae" greater than 5.6 mm ML were captured at depths shallower than 50 m, while smaller specimens were captured between 10 and 300 m, mostly at about 100 m. Eggs were reported from the upper 150 m in Hawaiian waters by Young et al. (1985).

REMARKS.—Young et al. (1985) present a detailed study of the eggs and "larvae" of an unidentified species of *Brachioteuthis* from Hawaiian waters. Other records of young forms are very scattered in the literature. Fewer than 10 species have been named. The family is in need of revision.

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Family CYCLOTEUTHIDAE Naef, 1923

(by K. Jefferts and C.F.E. Roper)

FAMILY CHARACTERS.—*Adults:* Buccal connectives attach to ventral borders of arms IV; arms with 2 rows of suckers; tentacular club with 4 rows of suckers, expanded with well-defined manus and dactylus; carpus ill-defined with up to about 7 knobs; funnel locking-cartilage oval or subtriangular with oblique groove anteriorly; fins (including tail when present) greater than 50% ML.

Young (7-8 mm ML): Funnel locking-cartilage subtriangular; 4 rows of suckers on tentacular club, more than 15 club suckers; tentacular stalk robust; tentacle length equal to or greater than ML; arms I-IV weakly muscular; eyes prominent, on short stalks, directed anteriorly, in *Discoteuthis* occupy nearly entire lateral surface of head.

REMARKS.—Young of *Discoteuthis* can be confused with young Octopoteuthidae because of general similarity of head shape, fin size, tissue consistency, and the presence of a few large suckers on the tentacular club. However, unlike the Octopoteuthidae, the Cycloteuthidae have the fin musculature separated in the midline by the gladius and more than 12 suckers on the club.

Key to Genera of CYCLOTEUTHIDAE (Young)

Fins short, ≤ 25% ML at 8.5 mm ML, never more than 75% ML (including tail); tail present in larger animals; manus suckers equal in size; arm formula $2 = 3 \geq 4 > 1$ . . . . . ***Cycloteuthis***

Fins long, 50% ML or more at 5 mm ML, grow to 100% ML in larger stages; no tail; manus suckers unequal in size; arm formula $2 \geq 3 > 4 > 1$ . . . . . ***Discoteuthis***

Cycloteuthis Joubin, 1919

GENERIC CHARACTERS.—*Adults:* Tail present; gladius thin, conus present; suckers on manus of equal size; photophores present on eyes and viscera; fins moderate (<100% ML).

GEOGRAPHICAL DISTRIBUTION.—Atlantic, South Africa to 39°N; Indian Ocean, Durban (S. Africa), and Albany (Australia).

Cycloteuthis sirventi Joubin, 1919

SPECIES CHARACTERS.—*Young* (Figure 201): Mantle elongate with small terminal fins; posterior tail a small bump between posterior margins of fins; visceral photophore barely visible, ventral to intestine; eyes protrude noticeably, not stalked; eye photophore not present; arms short; arm order $2 = 3 \geq 4 > 1$.

GEOGRAPHICAL DISTRIBUTION.—Throughout Atlantic warm waters.

VERTICAL DISTRIBUTION.—Clarke and Lu (1974, 1975) report captures during the day at 55-790 m (7 specimens) and at night at 700-785 m (1 specimen). Roper and Young (1975) report captures at 0-650 m during the day and 0-150 m during the night.

Cycloteuthis akimushkini Filippova, 1968

REMARKS.—Discussed by Clarke (1980); may be synonym of *C. sirventi*. The smallest known specimen is the holotype of 196 mm ML. The species occurs (as records from sperm whale stomachs) in the southern Indian Ocean; Durban, South Africa to Albany, Australia; and at 31°S in South Atlantic.

Discoteuthis Young and Roper, 1969

GENERIC CHARACTERS.—*Adults:* Tail absent; gladius thick, conus minute or absent; suckers on manus unequal-size; photophores present in integument; fins large (attain ≥100% ML).

GEOGRAPHICAL DISTRIBUTION.—Atlantic, 3°N to 33°N; South Pacific (Roper, unpublished data).

Discoteuthis discus Young and Roper, 1969

SPECIES CHARACTERS.—*Young* (Figure 202*e*): Mantle margin papillae absent; fins short, transversely oval; allometric changes in fin length (16 mm ML = 60% ML, 24-25 mm ML = 80%-90% ML, 45 mm ML = ≥98% ML).

GEOGRAPHICAL DISTRIBUTION.—Atlantic warm waters.

VERTICAL DISTRIBUTION.—Captured at 0-750 m during the day and 0-400 m during the night (Roper and Young, 1975).

Discoteuthis laciniosa Young and Roper, 1969

SPECIES CHARACTERS.—*Young* (Figure 202*a-c*): Mantle short, very broad in smallest larvae, proportionately narrower with growth; huge, broad, round fins (5 mm ML = ~50% ML, 9 mm ML = 80%-90% ML, 10-15 mm ML = >ML); fin width = 133%-160% ML; fins separated by broad pen; series of 6-8 papilla-like flaps project from ventral two-thirds of mantle margin; arms weak; arm formula $2 \geq 3 > 4 > 1$.

GEOGRAPHICAL DISTRIBUTION.—North Atlantic and Central Pacific warm waters.

VERTICAL DISTRIBUTION.—Undetermined; captures are from open nets.

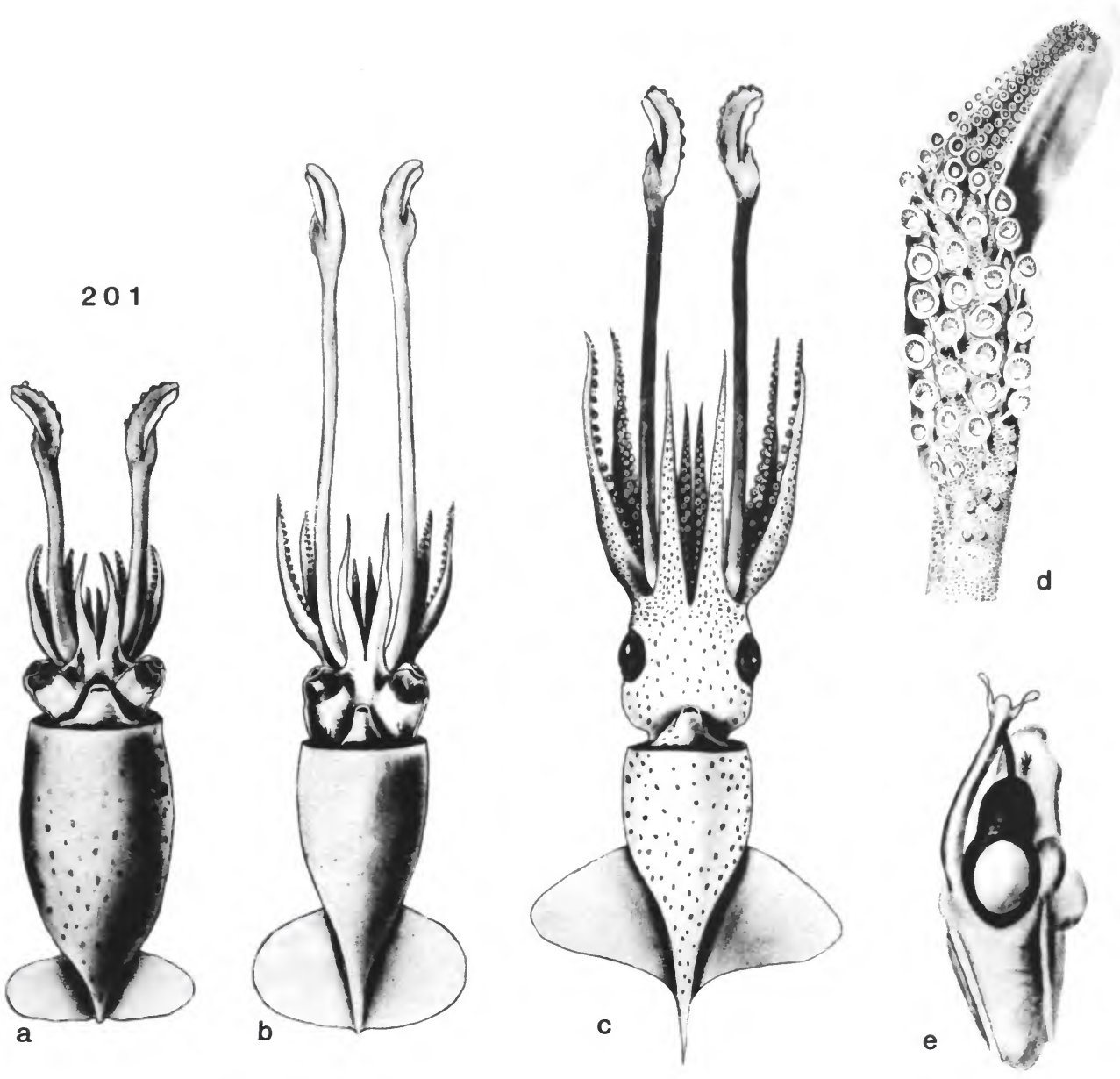

FIGURE 201.—*Cycloteuthis sirventi*, North Atlantic: *a*, ventral view, 8.5 mm ML; *b*, ventral view, 15 mm ML; *c*, ventral view, 27 mm ML; *d*, tentacular club, 42 mm ML; *e*, photophore on ink sac of same. (From Young and Roper, 1969.)

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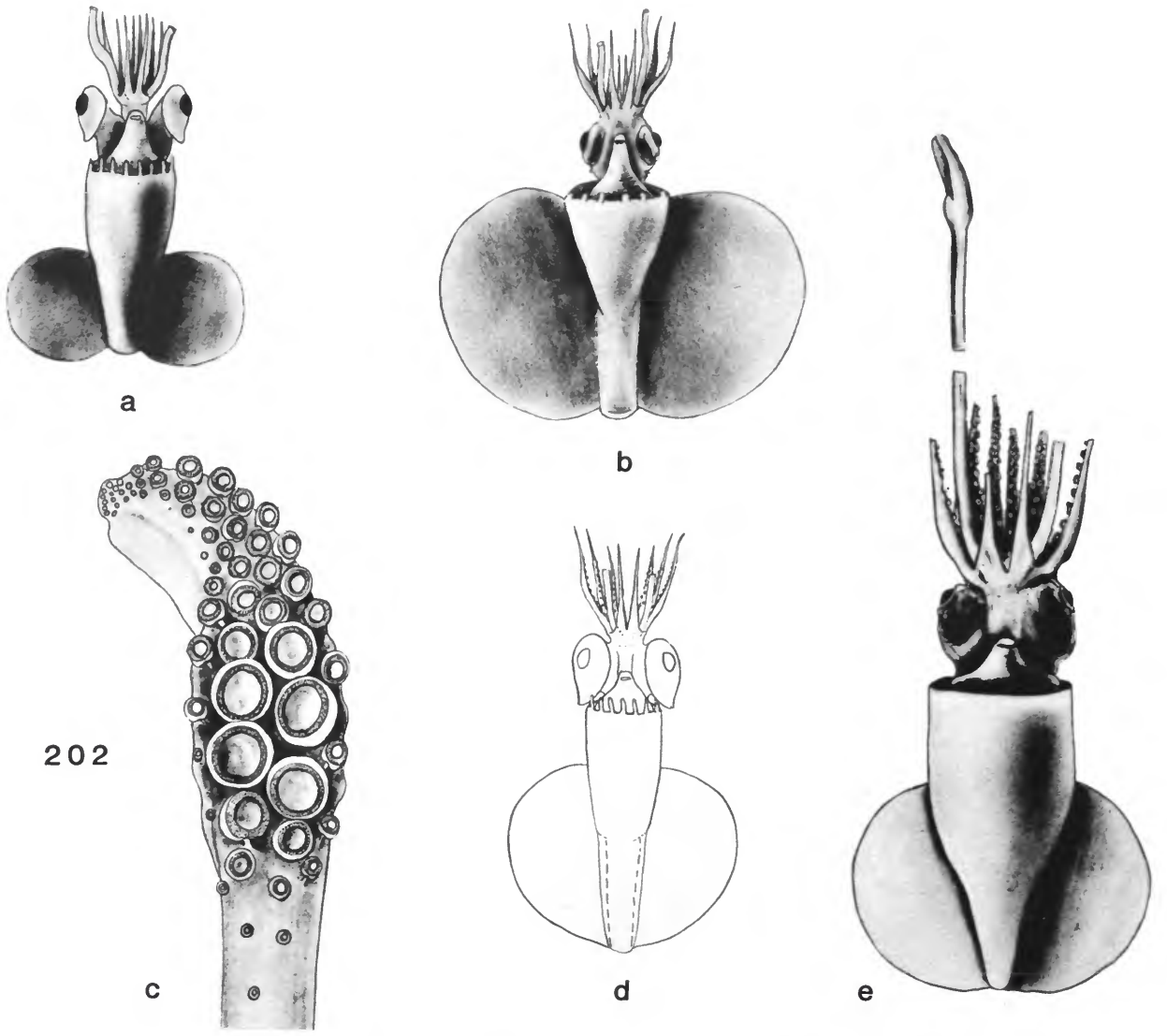

FIGURE 202.—*Discoteuthis* spp: *a–c, Discoteuthis laciniosa*, North Atlantic: *a*, ventral view, 5 mm ML; *b*, ventral view, 14 mm ML; *c*, tentacular club, 20 mm ML; *d, Discoteuthis* sp., ventral view, 9 mm ML; *e*, *Discoteuthis discus*, ventral view, 16 mm ML, 7°N, 46°W. (From Young and Roper, 1969.)

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Family OCTOPOTEUTHIDAE Berry, 1912

(by S.J. Stephen and K. Jefferts)

FAMILY CHARACTERS.—*Adults:* Tentacles absent; photophores on tips of at least some arms; 2 rows of hooks on arms; buccal connectives attach to ventral borders of arms IV; funnel locking-cartilage simple, straight, moderately broad; fins very long, occupy up to 100% ML.

Young: Tentacles present; tentacular clubs short, spatulate, with 8 suckers (several very large) in 2 rows; narrow pigmented keels extend laterally along each side of club; fins very broad in specimens >3 mm ML; photophores present on some arm tips by 3–5 mm ML (but arm tips frequently missing); in "larvae" all arms with suckers; funnel locking-cartilage straight.

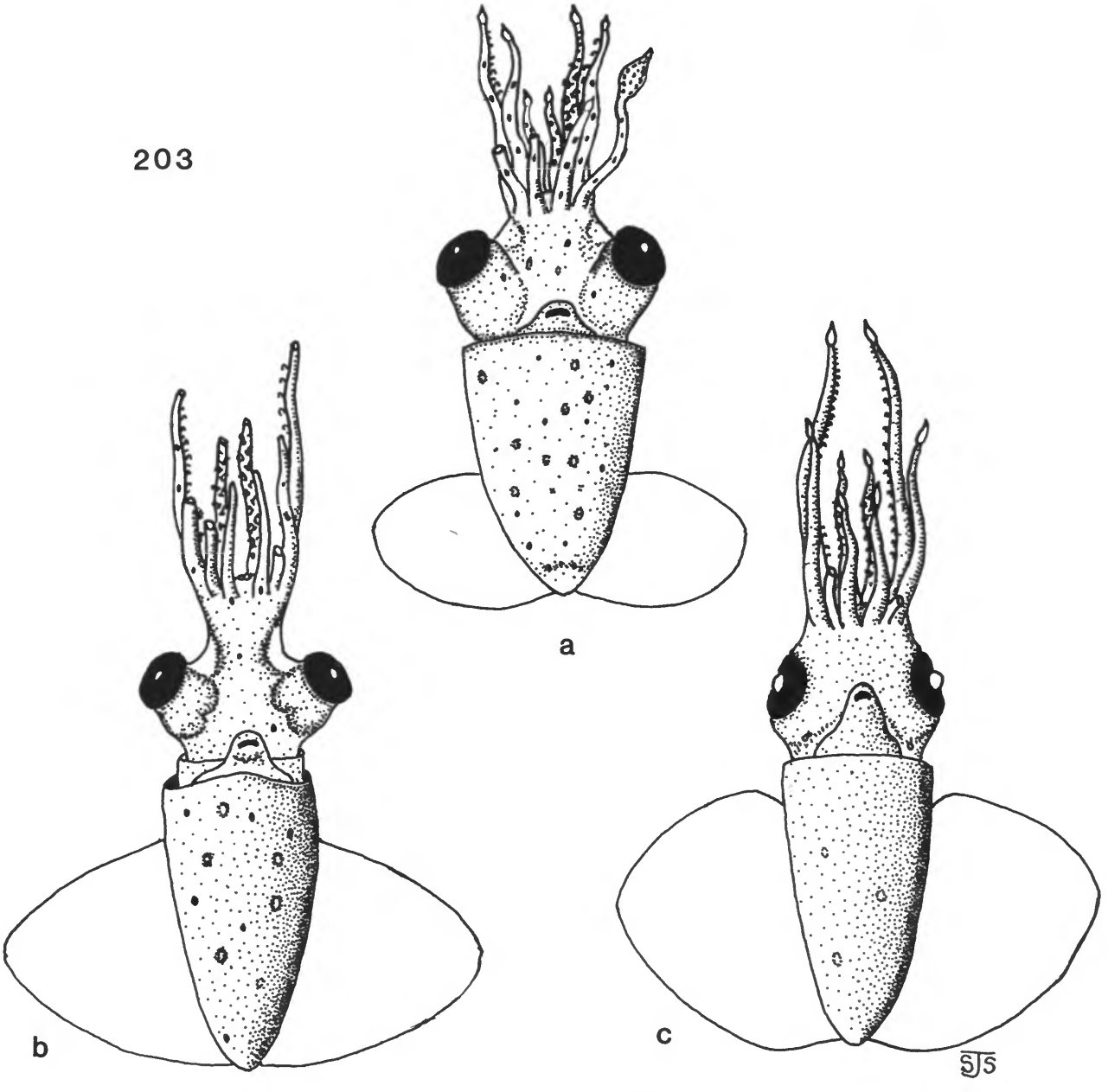

FIGURE 203.—*Octopoteuthis* sp., ventral view of developmental series: *a*, 4.5 mm ML; *b*, 6 mm ML; *c*, 8 mm ML. (From Stephen, 1985.)

Key to Genera of OCTOPOTEUTHIDAE (Juveniles)

Tentacles with weak, gelatinous stalks that are lost at sizes greater than 12 mm ML; when still present, tentacles longer than arms with up to about 8 proportionally large suckers; tentacle bases may be present up to about 25 mm ML; arms usually proportionally longer; some arm suckers develop into hooks by 2.5 mm ML in some species; paired photophores may develop on ink sac by 15 mm ML . . . . . ***Octopoteuthis***

Tentacles with robust stalks, clubs with 8 small suckers; tentacles much shorter than arms II (except longer at 2 mm ML in Hawaiian species), occur until about 38 mm ML before being lost; arms proportionally short, robust; no hooks develop before 5 mm ML; photophores develop only on arms II by 4.7 mm ML; large, single, median photophore on ink sac by 5 mm ML . . . . . ***Taningia***

Octopoteuthis Ruppell, 1844

GENERIC CHARACTERS.—*Young* (Figure 203): Mantle short, conical, with gelatinous outer layer; funnel short initially, extending to between eyes by 10 mm ML; gelatinous tissue layer on head gives smaller specimens appearance of short arm-crown stalk and short, wide eye-stalks; fins very wide (apparent as small as 2.5 mm ML), length approaching 100% ML by 10 mm ML; all arms bear single photophore at distal tip; paired photophores on ink sac.

GEOGRAPHICAL DISTRIBUTION.—Worldwide from 56°N to 50°S.

VERTICAL DISTRIBUTION.—Oceanic; young occur in near-surface waters (primarily 0–300 m) and adults are meso- to bathypelagic.

REMARKS.—The genus, currently being revised by S. Stephen, is composed of at least five species. Co-occurence of four congeners is common over the range of the genus in subtropical and North Atlantic temperate waters.

Taningia Joubin, 1931

GENERIC CHARACTERS.—*Young* (Figure 204): Mantle short, conical, with gelatinous outer layer; fins very wide, length approaching 100% ML by 3 mm ML; arms II with single photophore on distal tips; single median photophore on ink sac.

GEOGRAPHICAL DISTRIBUTION.—Worldwide from 40°N to 40°S.

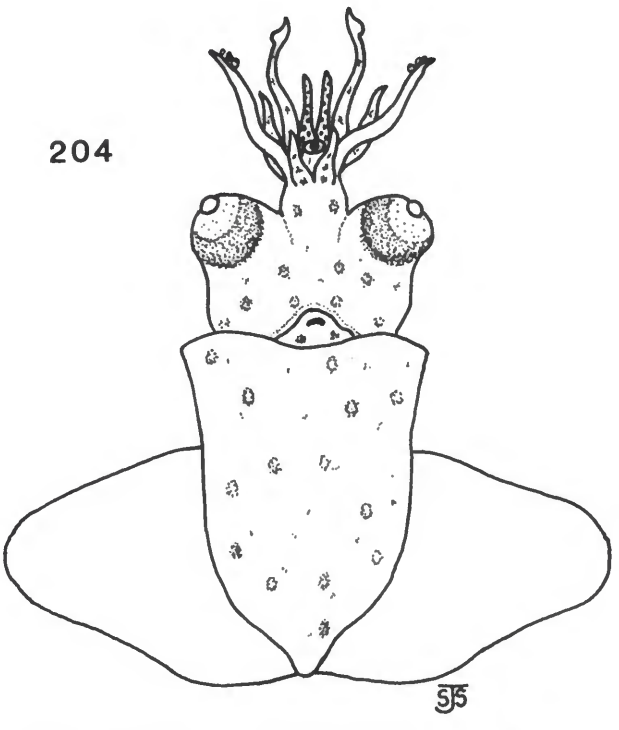

FIGURE 204.—*Taningia danae*, ventral view, 2 mm ML. (Original drawing.)

VERTICAL DISTRIBUTION.—Oceanic; young occur in near-surface waters (primarily 0–300 m) and adults inhabit the deep sea.

REMARKS.—The genus is monotypic; *Taningia danae* Joubin, 1931 (see Clarke, 1967). This species is important in the diet of sperm whales and other odontocetes (Clarke, 1987).

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Family LEPIDOTEUTHIDAE Pfeffer, 1912

(by M.R. Clarke)

FAMILY CHARACTERS.—*Adults* (Figure 205): Tentacles lost in adults; 2 rows of suckers on arms; leathery, rhomboidal scales over mantle except on posterior region between fins ventrally; fins not scaled or lobed, together form oval shape with long axis along longitudinal axis of body; posterior half of gladius with dorsal, axial, cartilaginous rod enveloped by chitinous conus to form tube; photophores absent; funnel locking-apparatus elongate with short, straight groove, deeper anteriorly; buccal connectives attach to ventral borders of arms IV (Clarke and Maul, 1962; Joubin, 1900).

Young: At approximately 60 mm ML: tentacles present, very small, with 6 sucker-like structures on slightly expanded clubs; mantle covered with small papillae, precursors of scales, with 2–4 minute "cartilaginous" points on each papilla (Clarke, 1964).

GEOGRAPHICAL DISTRIBUTION.—Adults or flesh from adults were all collected from stomachs of sperm whales caught in the Atlantic from 40°N to 40°S, the southern Indian Ocean (Clarke, 1980), and Japan (Okutani et al., 1976), and from stomachs of fish caught in the western Pacific (Rancurel, 1970).

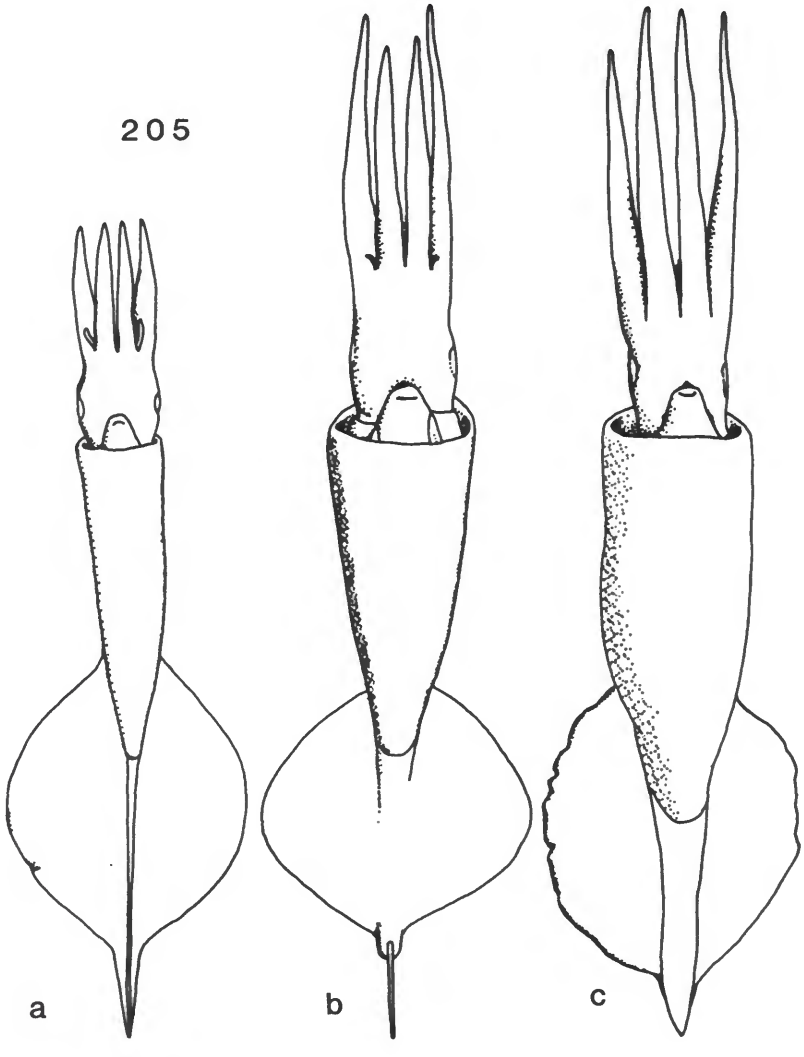

FIGURE 205.—*Lepidoteuthis grimaldii*, ventral view of growth series: *a*, 60 mm ML; *b*, 85 mm ML; *c*, 970 mm ML. (From Clarke, 1964.)

VERTICAL DISTRIBUTION.—Young were captured in opening-closing nets fished at 23–50 m and 100–270 m (Clarke and Lu, 1974; Lu and Clarke, 1975) in the North Atlantic at 11°N and 30°N and in an open net at 0–245 m at 32°N (Clarke, 1964).

REMARKS.—Only five juveniles have been collected with the following MLs: 29, 39, 60, 78, and 85 mm. Between 60 mm and 85 mm ML, a distinct change takes place in body proportions involving a broadening of the mantle and elongation of the arms (Figure 205*a,b*). The family is monotypic; *Lepidoteuthis grimaldii* Joubin, 1895 is the only known species.

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Family PHOLIDOTEUTHIDAE Adam, 1950

(by M.R. Clarke)

FAMILY CHARACTERS.—*Adults* (Figures 206*a*, 207): Small papillae or scales cover mantle except for posterior end of body between fins ventrally; fins with anterior lobes, rhomboid in shape; 2 rows of suckers on arms; tentacles moderately long with slightly expanded clubs; suckers in 4 rows, each sucker compressed with a characteristically slit-like opening with prominent peg-like teeth on infundibulum; gladius with short posterior conus; buccal connectives attach to ventral borders of arms IV.

Young (Figure 206*d*): 14 mm ML: club suckers crowded in 4 rows, but not compressed and without sucker-free area between 2 medial rows (as in larger specimen above); dermal scales as above; other features as adult. 32.8 mm ML: dermal scales with small papillae around margins (as described for *Tetronychoteuthis massyae* by Pfeffer, 1912); club suckers as in adult *Pholidoteuthis*.

GEOGRAPHICAL DISTRIBUTION.—Gulf of Mexico (Voss, 1956), North Atlantic to 40°S in Atlantic, South Indian Ocean (Clarke, 1980), western Pacific (Adam, 1950; Rancurel, 1970).

VERTICAL DISTRIBUTION.—Eight young (9.9–15.6 mm ML) named *Tetronychoteuthis massyae* and probably attributable to *Pholidoteuthis* were caught at 23–50 m at 11°N, 20°W (Lu and Clarke, 1975).

REMARKS.—Two species have been well described, *Pholidoteuthis boschmai* Adam, 1950 (Figure 206*a–c*), and *P. adami* Voss, 1956 (Figure 207). The relationship and validity of the species *Tetronychoteuthis dussumieri* (Orbigny, 1839) and *T. massyae* Pfeffer, 1912 are not clear and have been discussed elsewhere (Clarke, 1980). The discovery of specimens with scales like *T. massyae* Pfeffer, 1912 and tentacular club suckers like *Pholidoteuthis* clearly shows that the species *T. massyae* belongs to the same genus as *Pholidoteuthis boschmai* Adam.

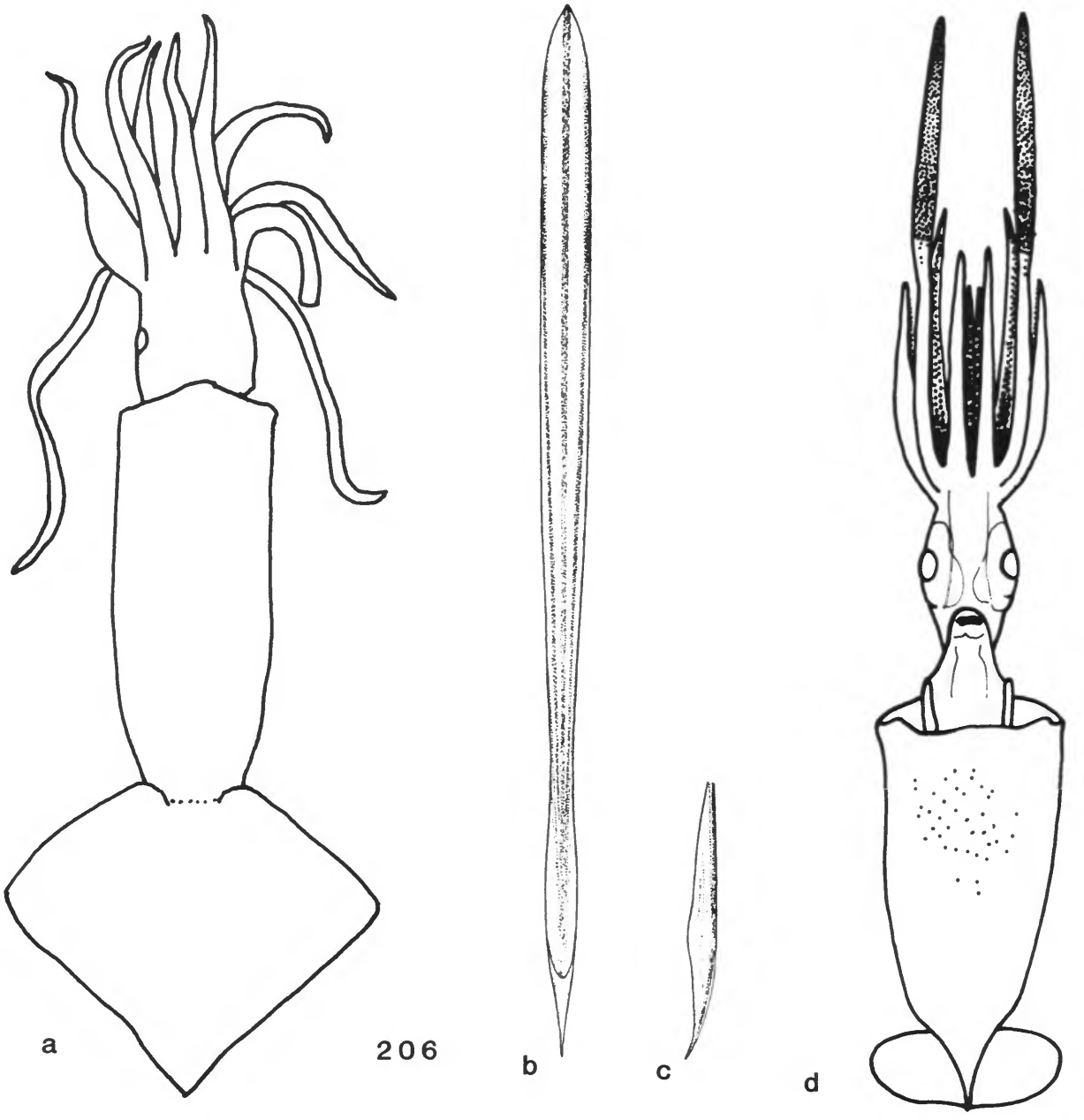

FIGURE 206.—*a–c, Pholidoteuthis boschmai: a,* dorsal view, holotype, 273 mm ML (redrawn from Adam, 1950); *b,* gladius of same; *c,* lateral view of conus of same (*b,c,* from Adam, 1950). *d, Pholidoteuthis* sp. ventral view, 14 mm ML (original drawing).

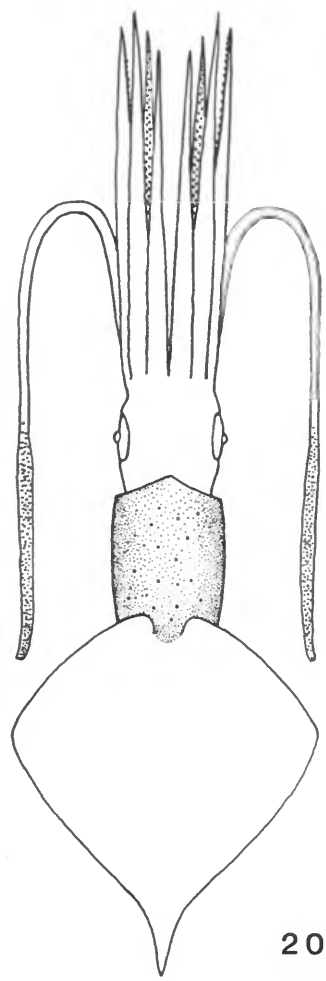

FIGURE 207.—*Pholidoteuthis adami*, dorsal view, 136 mm ML, Gulf of Mexico. (From Voss, 1956.)

Voss (1956) distinguished his Gulf of Mexico species from Adam's East Indies species (*P. boschmai*) on the basis of the fin shape.

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Family BATOTEUTHIDAE Young and Roper, 1968

(by C.F.E. Roper and M.J. Sweeney)

FAMILY CHARACTERS.—*Adults* (Figure 208*a–c*): Arms with 2 rows of suckers; tentacular clubs very elongate with 6 longitudinal rows of suckers; buccal connectives attach to ventral borders of arms IV; funnel locking-cartilage a simple, straight groove; posterior end of mantle drawn out into long, pointed tail.

Young (Figure 208*d*): Mantle sac-like, membranous, transparent; mantle opening flares (considerably wider than head); fins extremely small, broadly ovoid, with no free lobes; tail extremely long, needle-like; head very narrow, small; funnel large, extends to level of anterior border of eyes; sucker bearing portion of tentacles approximately 90% of tentacle length; clubs as in adults. Smaller specimens unknown.

GEOGRAPHICAL DISTRIBUTION.—Northern portion of Antarctic Ocean (50°S–60°S) in the Pacific sector and a portion of the Atlantic sector (~55°W–170°W); range limits undetermined.

VERTICAL DISTRIBUTION.—Oceanic, known only from original open-net captures between 366 m and 2525 m.

REMARKS.—Monotypic family; *Batoteuthis skolops* Young and Roper, 1968.

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Family CHIROTEUTHIDAE Gray, 1849

(by C.F.E. Roper and M.J. Sweeney)

FAMILY CHARACTERS.—*Adults:* Funnel locking-cartilage oval with one or two inward projecting knobs (ventral tragus and posterior antitragus); arms with 2 rows of suckers; tentacles very long, slender with suckers in 4 rows; buccal connectives attach to ventral borders of arms IV; photophores usually present (may be on eyes, ventral arms, tentacles, clubs, viscera); fins together round or oval; secondary fin may be present.

Young: Neck long, columnar, vesiculate; arm-crown stalk long (variable among species); gladius extends well posterior to fins (frequently broken); small secondary fins posterior to primary fins, but frequently lost (presence in *Chiroteuthis* verified); ventral arms become very elongate, robust (not in smallest specimens); tentacles develop early with very elongate, thick stalks; clubs short with 4 rows of small suckers; digestive gland cylindrical, lies along body axis. Known as *Doratopsis* larva.

GEOGRAPHICAL DISTRIBUTION.—Representatives of the family are found in all oceans except in northern high latitudes.

VERTICAL DISTRIBUTION.—Off California the youngest specimens of *Chiroteuthis calyx* examined (20–30 mm ML) were found in the upper 100 m; 30–50 mm ML specimens were most abundant in 300–400 m; and 40–60 mm ML specimens predominated in the 500–700 m stratum (Roper and Young, 1975).

REMARKS.—Mantle length in this family is measured to posterior end of fins. Secondary fins not verified in *Valbyteuthis* and *Asperoteuthis*, but nature of broken gladius/tail suggests their presence. At present, several additional nominal genera are suspected (Nesis, 1980), but because the family is under revision by C. Roper and R. Young, only clearly distinguished "genera" and species are considered (see Roper and Young, 1967).

Key to Genera of CHIROTEUTHIDAE (Adults, Subadults, and Late Juveniles)

1. Mantle covered with numerous minute "cartilaginous" tubercles; fins together oval to elongate/oval with long axis longitudinal; arms IV no longer or thicker than arms II and III. Subadult . . . . . ***Asperoteuthis***
   No tubercles on mantle; fins together form outline either circular or oval with long axis transverse to body; arms IV longer than arms II and III 2
2. Fins together roughly oval in outline with long axis transverse to mantle and lobed posteriorly as well as anteriorly; arms IV not much thicker than arms II and III; funnel valve absent; funnel locking-apparatus without tragus . . . . . ***Valbyteuthis***
   Fins together approximately circle-shape, not lobed posteriorly; arms IV usually much thicker than arms II and III; funnel valve present; distinct tragus present on funnel locking-apparatus . . . . . ***Chiroteuthis***

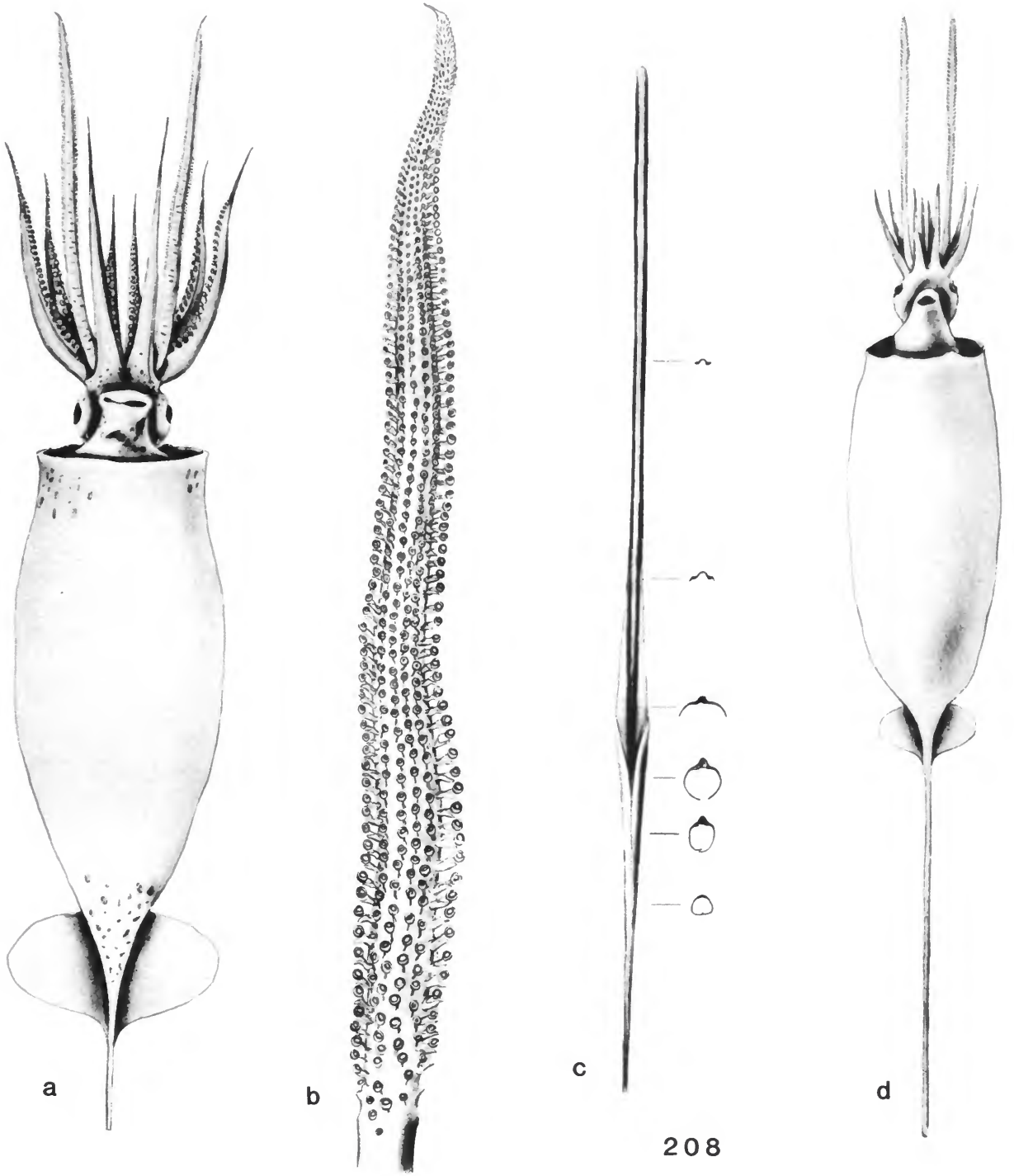

FIGURE 208.—*Batoteuthis skolops*, Antarctic: *a*, ventral view, holotype, 51 mm ML; *b*, tentacular club of same; *c*, gladius of female, 95 mm ML; *d*, ventral view, 30 mm ML. (From Young and Roper, 1968.)

Chiroteuthis Orbigny, 1841 [in 1834–1848]

GENERIC CHARACTERS.—*Young* (Figure 209): Mantle slender, long, spindle-shape; fins round with length of fin insertion equal to length of fin (i.e., weak lobes); arm-crown stalk short relative to neck length; arms IV very elongate, robust (>11 mm ML); clubs relatively long with suckers on long stalks on oral surface at base, or entire oral surface with minute suckers, mostly in 4 rows, or oral surface naked; photophores develop on ventral surface of eyes, ink sac, ventral arms, tentacular stalks, club tips; funnel valve present; funnel locking-apparatus with tragus and antitragus. "Larval" features

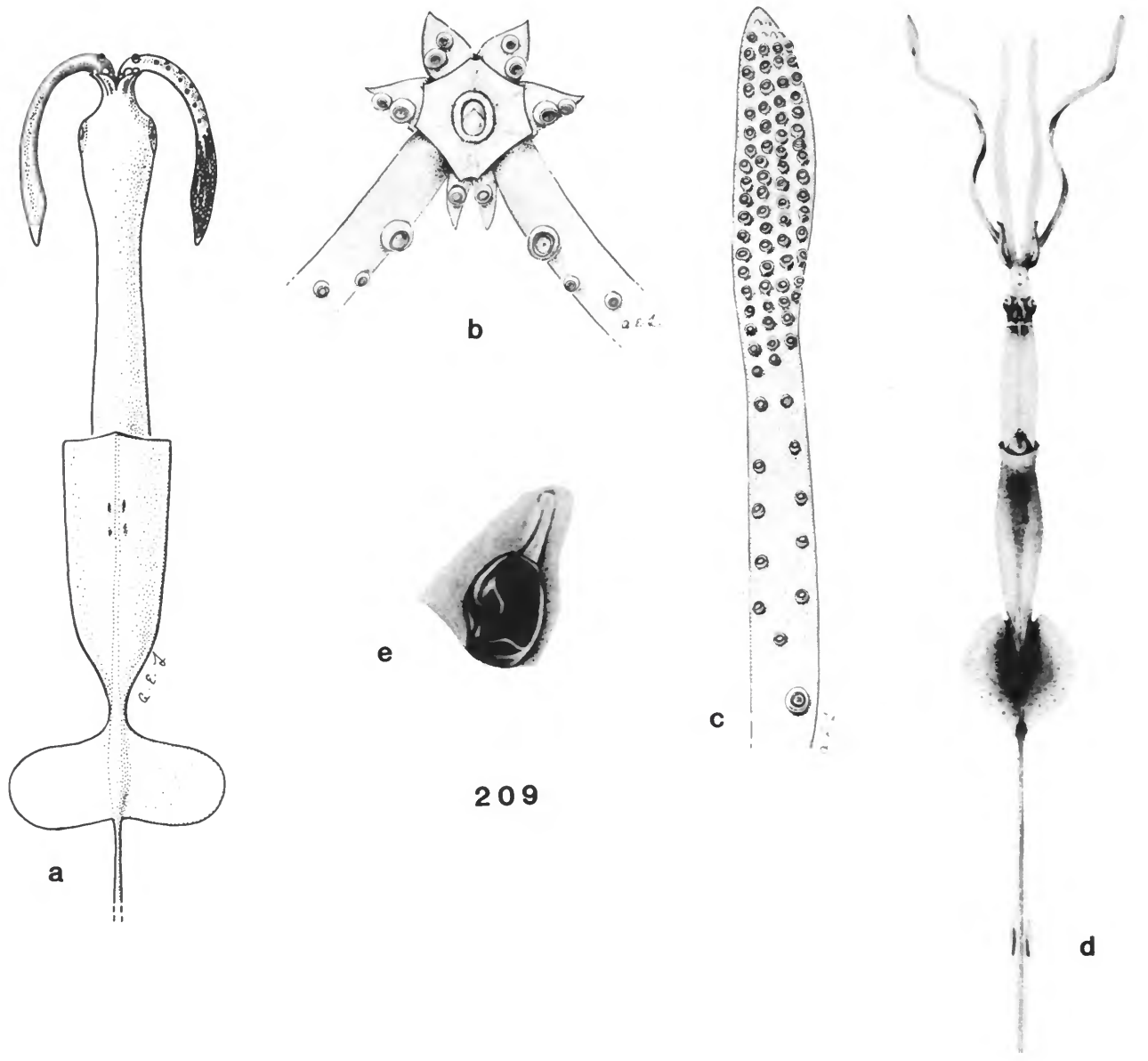

FIGURE 209.—*Chiroteuthis* sp.: *a*, dorsal view, North Atlantic, 5.6 mm ML; *b*, oral view of same; *c*, tentacle of same (*a–c*, original drawings); *d*, ventral view, 37.5 mm ML; *e*, funnel locking-component of same (*d,e*, from Pfeffer, 1912).

retained to at least 76 mm ML in some species.

GEOGRAPHICAL DISTRIBUTION.—Worldwide except high latitudes.

VERTICAL DISTRIBUTION.—Meso- to bathypelagic.

Valbyteuthis Joubin, 1931

GENERIC CHARACTERS.—*Young* (Figure 210*a,b*): Mantle relatively broad, goblet-shape; fins round with length of fin insertion less than length of fin (i.e., pronounced anterior and posterior lobes); arm-crown stalk often as long as or longer than neck; arms IV elongate (>15 mm ML); tentacle stalks naked (without suckers or knobs); clubs relatively short with suckers on short stalks in 4 rows; photophores absent; funnel valve absent; tragus absent. "Larval" features retained up to at least 55 mm ML.

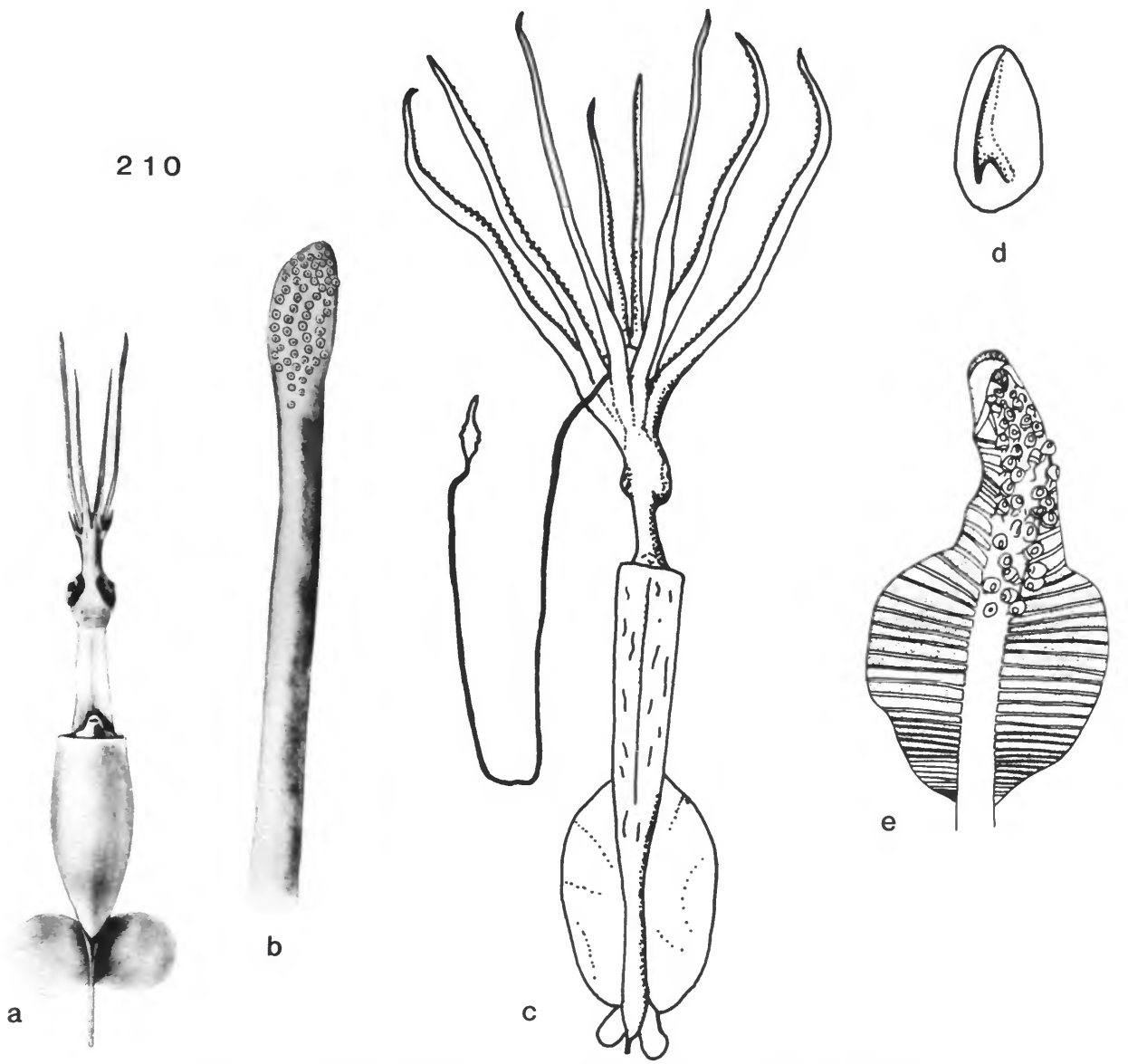

FIGURE 210.—*a,b, Valbyteuthis* sp., eastern Pacific: *a*, ventral view, 15 mm ML; *b*, tentacle of same (*a,b*, from Roper and Young, 1967). *c–e, Asperoteuthis* sp.: *c*, ventral view, 188 mm ML; *d*, funnel locking component of same; *e*, tentacular club of same (*c–e*, after Lu, 1977, as *Chiroteuthis acanthoderma*).

GEOGRAPHICAL DISTRIBUTION.—Tropical and temperate waters in all oceans.

VERTICAL DISTRIBUTION.—Bathypelagic (rarely mesopelagic).

Asperoteuthis Nesis, 1980

GENERIC CHARACTERS.—*Young* (Figure 210*c–e;* subadult): Mantle elongate, slender; fins elongate, oval, lobes absent; arms IV no wider than and subequal to arms III and II; arms I shorter; tentacle stalks with numerous knobs along aboral surface; tentacular stalk suckers unknown; clubs relatively short, suckers in 4 rows; "cartilaginous" tubercles cover surface of mantle, head, and arms; funnel valve present; tragus indistinct; photophores present on tentacular stalk, absent on ventral arms and ink sac. Monotypic genus; *Asperoteuthis famelica* (Berry, 1909).

GEOGRAPHICAL DISTRIBUTION.—Central waters of North Pacific Ocean.

VERTICAL DISTRIBUTION.—Meso- to bathypelagic.

Key to Genera* of CHIROTEUTHIDAE ("Larvae")

Mantle long, slender, spindle-shape; arm-crown stalk short relative to neck length; clubs relatively long with suckers on long stalks in 4 rows; tentacular stalks with few or many suckers on oral surface (rarely naked) . . . . ***Chiroteuthis***

Mantle relatively broad, goblet-shape; arm-crown stalk often as long as or longer than neck; clubs relatively short with suckers on very short stalks in 4 rows; tentacular stalks naked . . . . . ***Valbyteuthis***

* *Asperoteuthis* "larvae" presently unknown; "cartilaginous" tubercles and tentacular knobs probably appear quite early in development.

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1931. Notes preliminaires sur les cephalopodes des croisieres du *Dana* (1921–1922), 3e partie. *Annales de l'Institut Oceanographique,* 10(7):169–211.

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Family MASTIGOTEUTHIDAE Verrill, 1881

(by C.F.E. Roper and M.J. Sweeney)

FAMILY CHARACTERS.—*Adults:* Funnel locking-cartilage oval with inward projecting knobs, as in Chiroteuthidae, but posterior antitragus generally weakly developed; occasionally medial tragus also poorly developed, giving locking-cartilage an almost oval appearance; tentacles long, whip-like with many hundreds of minute suckers in more than 15 rows; 2 rows of suckers on arms; buccal connectives attach to ventral borders of arms IV; ventral arms (IV) commonly enlarged; small photophores (sometimes very numerous) often embedded in integument of mantle, fins, head, and arms; small photophore occasionally on eye or eyelid; fins generally large.

Key to Genera of MASTIGOTEUTHIDAE (Adults, Subadults, and Juveniles)

Mantle, head, funnel, and arms covered by numerous, small, cartilage-like tubercles . . . . . ***Echinoteuthis***

Mantle, head, funnel, and arms smooth or covered with low papillae . . . . . ***Mastigoteuthis***

Mastigoteuthis Verrill, 1881

GENERIC CHARACTERS.—*Young* (Figure 211): Mantle elongate; fins transversely oval; tentacular club with >4 rows of suckers (6 mm ML); tentacular stalk thicker than arms; stalk and club circular in cross section; club not expanded; eyes at front of head project diagonally anteriorly; gladius extends well posterior to fins as long, spike-like tail.

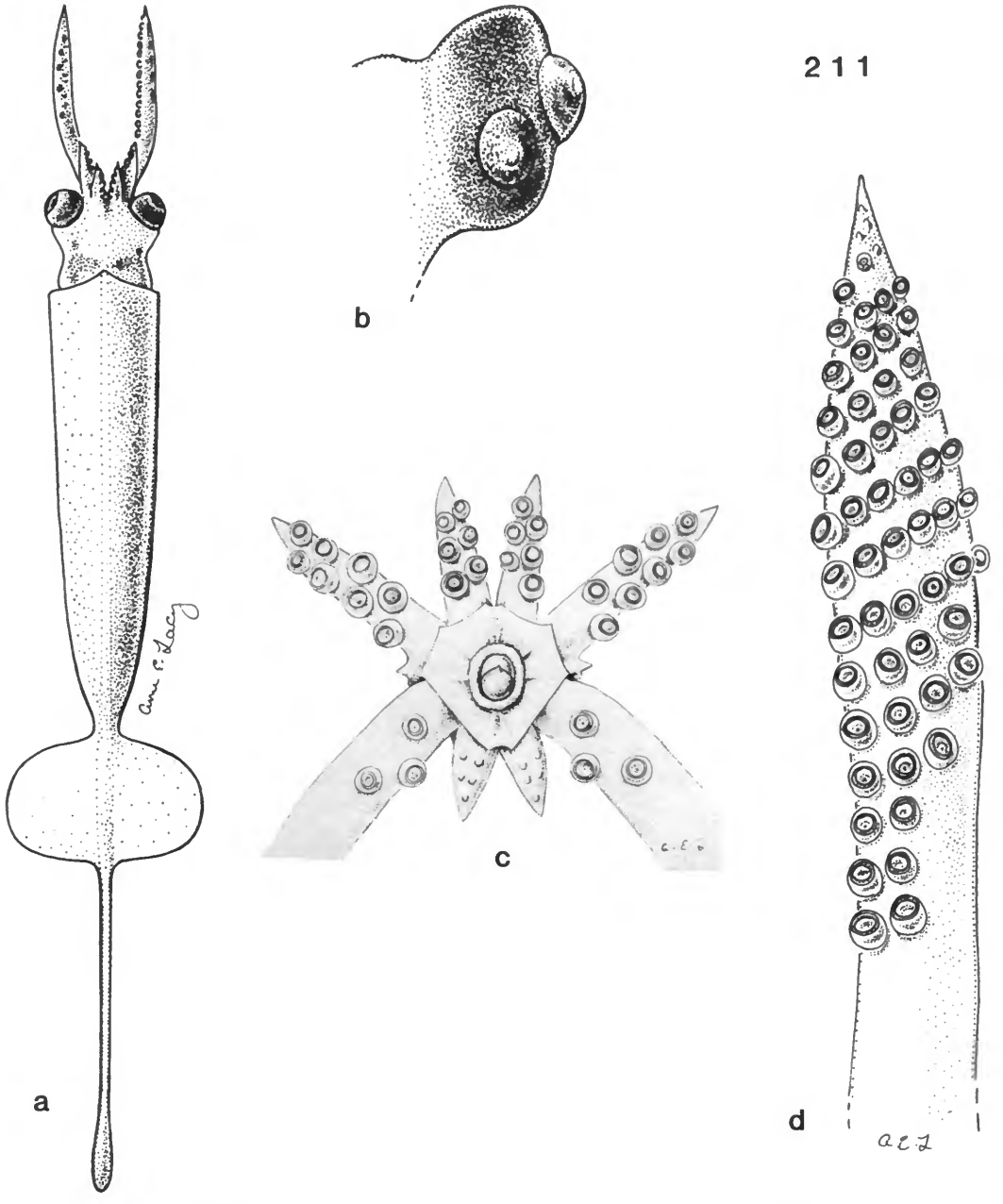

FIGURE 211.—*Mastigoteuthis cf. hjorti*, northwest Atlantic, USNM 730521, 6.0 mm ML: *a*, dorsal view; *b*, eye photophore of same; *c*, oral view of same; *d*, tentacular club of same. (Original drawing.)

GEOGRAPHICAL DISTRIBUTION.—*Mastigoteuthis* occurs worldwide in oceanic waters from tropical to boreal regions.

VERTICAL DISTRIBUTION.—Closing net data are available on vertical distribution for *M. schmidti* in the eastern North Atlantic (Clarke and Lu, 1975; Lu and Clarke, 1975), *M. pyrodes* from California and *M. hjorti* off Bermuda (Roper and Young, 1975). All the species show a distribution concentrated at 500–1000 m in daytime and ascending to shallower depths at night (even to 50–100 m).

REMARKS.—Many of the 15 or more nominal species were

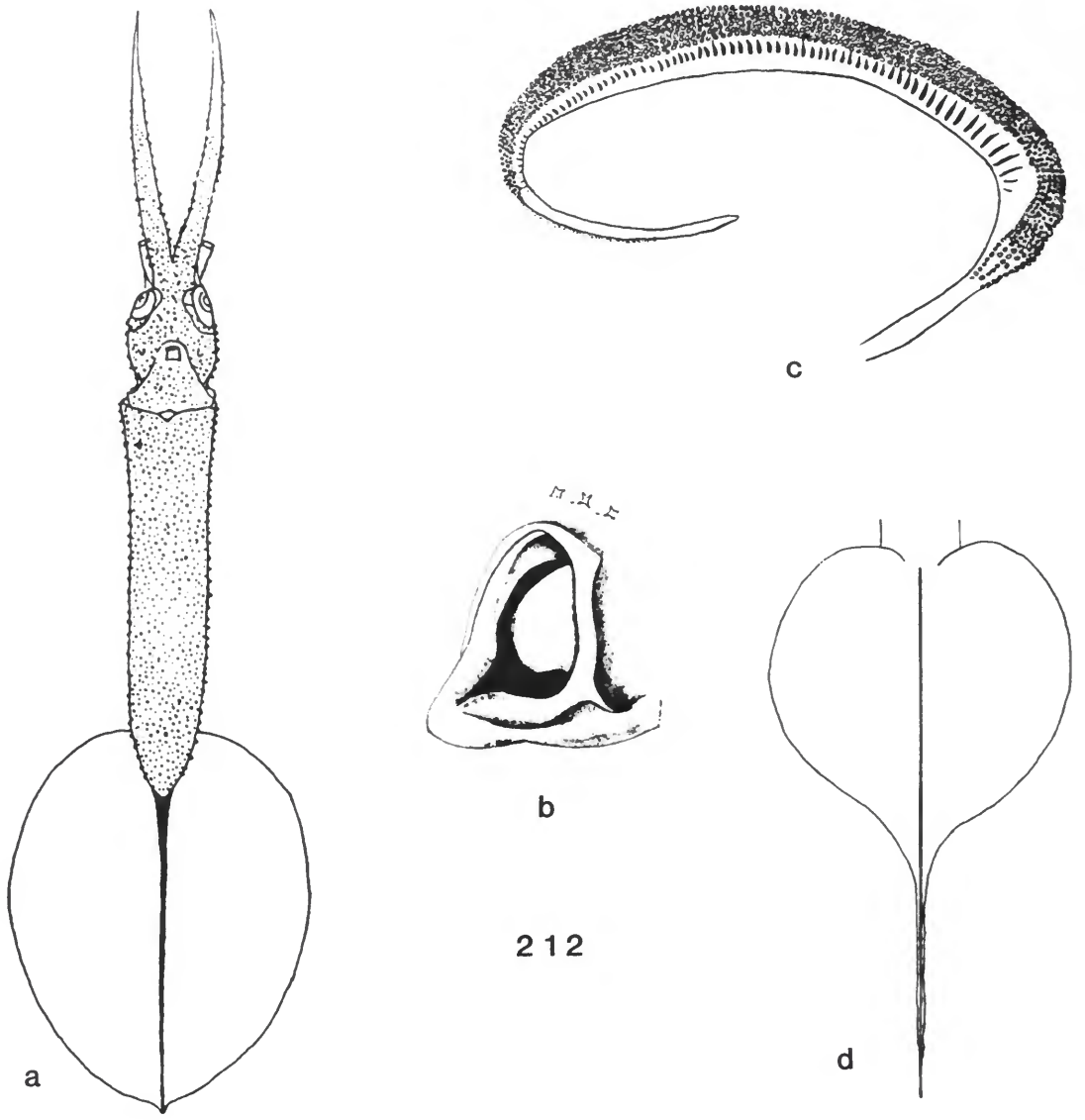

FIGURE 212.—*Echinoteuthis* sp., North Atlantic: *a*, ventral view, 40 mm ML, 35°N, 33°W; *b*, funnel locking-cartilage of same; *c*, tentacular club, 30 mm ML, 16°N, 62°W; *d*, fin of same. (From Joubin, 1933.)

described from specimens in poor condition. The genus is in need of revision (Young, 1972).

Echinoteuthis Joubin, 1933

GENERIC CHARACTERS.—*Young* (Figure 212) (Smallest described specimen 17 mm total length, approximately 11 mm ML, with form similar to largest specimen, 61 mm TL, 40 mm ML): Mantle very elongate, narrow; fins heart-shape to elongate/oval; tentacles with >4 rows of numerous, minute suckers; tentacular stalk circular in cross section; broad protective membrane with distinctive row of oblong chromatophores border manus; dactylus with very minute suckers; eyes at front of head, diagonally oriented; gladius extends far posterior to fins; cartilaginous spiny tubercles occur all over body, head, and arms in the larger specimens (30 and 40 mm ML), but only the first traces visible in juvenile of about 11 mm ML.

GEOGRAPHICAL DISTRIBUTION.—The single species of *Echinoteuthis*, *E. danae*, has not been reported since its original description based on three specimens caught near the Azores and the Antilles (Joubin, 1933).

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1972. The Systematics and Areal Distribution of Pelagic Cephalopods from the Seas Off Southern California. *Smithsonian Contributions to Zoology*, 97:1-159.

Family JOUBINITEUTHIDAE Naef, 1922

(by C.F.E. Roper and M.R. Clarke)

FAMILY CHARACTERS.—*Adults* (Figure 213*a,b*): Mantle cylindrical, elongate; arms I–III extremely long with 6 longitudinal rows of suckers; ventral arms much shorter with 4 longitudinal rows of suckers; tentacular clubs elongate, laterally compressed, with numerous, minute suckers arranged in 8–12 transverse rows; funnel locking-cartilage oval without tragus or antitragus; buccal connectives attach to ventral borders of arms IV; conus of gladius elongate with ventral fusion; tail elongate, filiform, longer than mantle; photophores absent; hectocotylus absent.

Young: Essentially as adults (Figure 213*c*) but arms and tentacles proportionally shorter; sucker bearing part of tentacles much shorter; skin bulges on median third of tail (possible remains of small secondary fin).

REMARKS.—Specimens from the northeastern Atlantic as small as 10.4 mm ML have been reported (Clarke and Lu, 1974) but not yet described; their characteristic long arms, cylindrical mantle, and long tail make identification easy.

Joubiniteuthis Berry, 1920

GENERIC CHARACTERS.—Family is monotypic; generic characters are as given for family.

Joubiniteuthis portieri (Joubin, 1916)

SPECIES CHARACTERS.—*Adults* and *Young:* With characters of the family.

GEOGRAPHICAL DISTRIBUTION.—North and South Atlantic, 30°N–30°S; western North Pacific off Japan.

VERTICAL DISTRIBUTION.—An oceanic deep-sea species captured from the near-surface waters to over 2000 m.

REMARKS.—Family monographed by Young and Roper (1969) with subsequent records and vertical distribution from Clarke and Lu (1974, 1975) and the first record in the Pacific from Okutani and Kubota (1972). *Valdemaria danae* Joubin, 1931 is a synonym.

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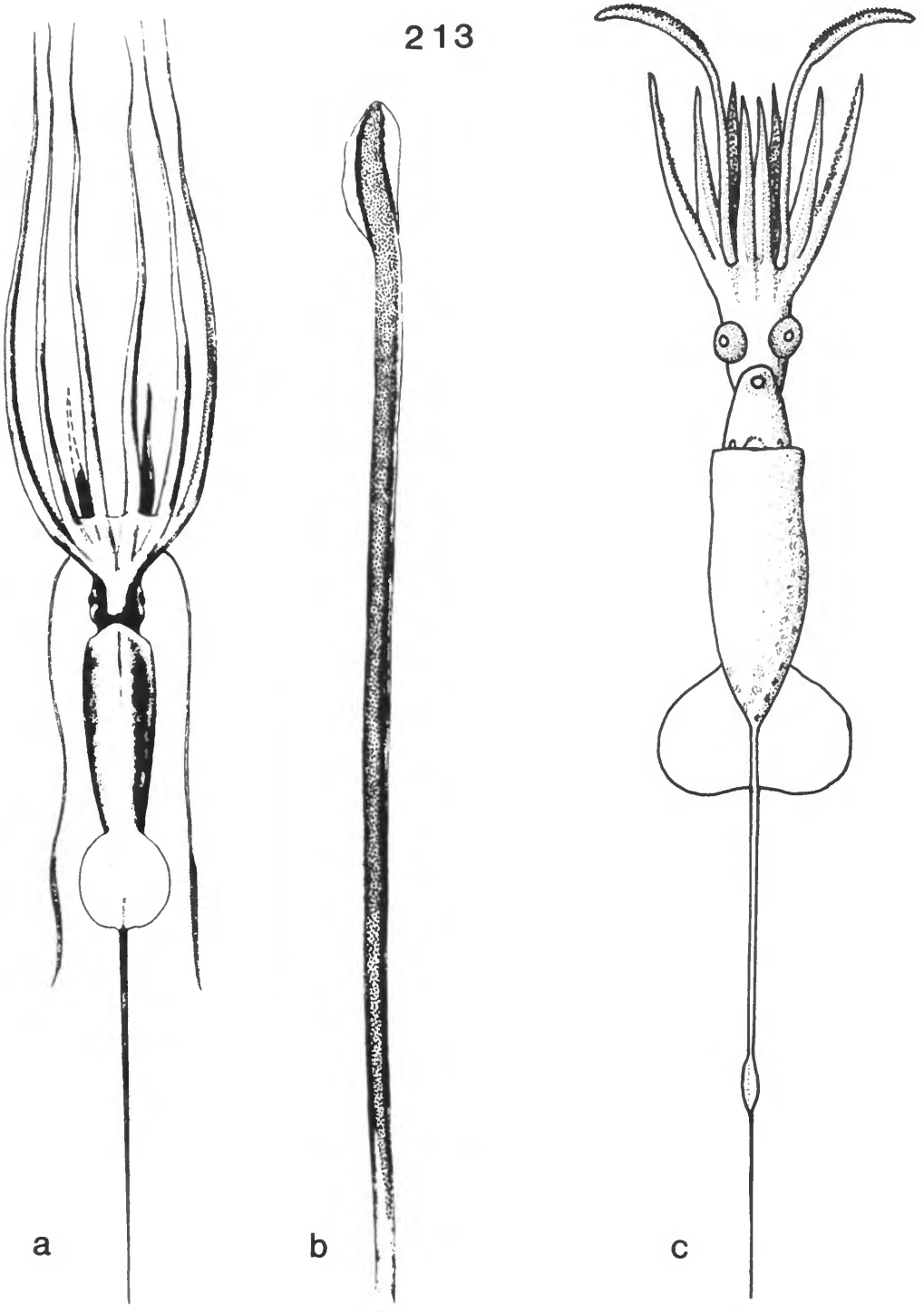

FIGURE 213.—*a,b, Joubiniteuthis portieri: a,* dorsal view, 89 mm ML, western North Atlantic; *b,* tentacular club of same (both from Young and Roper, 1969). *c, Joubiniteuthis* sp., ventral view, 10.6 mm ML, eastern North Atlantic (original drawing by Clarke).

Family GRIMALDITEUTHIDAE Pfeffer, 1900

(by M.R. Clarke)

FAMILY CHARACTERS.—*Adults* (Figure 214*a*): Funnel and mantle locking-cartilages fused; dorsal mantle-nuchal apparatus free; tentacles absent in adults; 2 rows of suckers on arms; buccal connectives attach to ventral borders of arms IV; mantle soft, gelatinous, transparent; tail very long with accessory fin (fragile, often missing); photophores may be present on tips of arms.

REMARKS.—Monogeneric family with two nominal species usually considered synonyms.

Grimalditeuthis bonplandi Joubin, 1898

SPECIES CHARACTERS.—*Young* (Figure 214*b*): Young not known. Grimpe (1925) considered *Enoptroteuthis spinicauda* Berry, 1920 a young specimen of *G. bonplandi*.

GEOGRAPHICAL DISTRIBUTION.—Reported from Atlantic, Gulf of Mexico, and central Pacific. Zuev and Nesis (1971) mention an undescribed species from the Antarctic Ocean.

VERTICAL DISTRIBUTION.—Data available from the Atlantic are for closing nets in daylight at 200–250 m (11°N) and 910–1020 m (18°N), and at night at 805–900 m (11°N) and 1000–1500 m (18°N) (Lu and Clarke, 1975; Clarke and Lu, 1975); and for open-net captures of 4 specimens >46 mm ML, 2100–0 m at night (Roper and Young, 1975). Closing-net data are available from off Hawaii for night (3 specimens 20–30 mm ML, upper 300 m) and for day (2 specimens 60–80 mm ML, 750 m and 1275 m) (Young, 1978).

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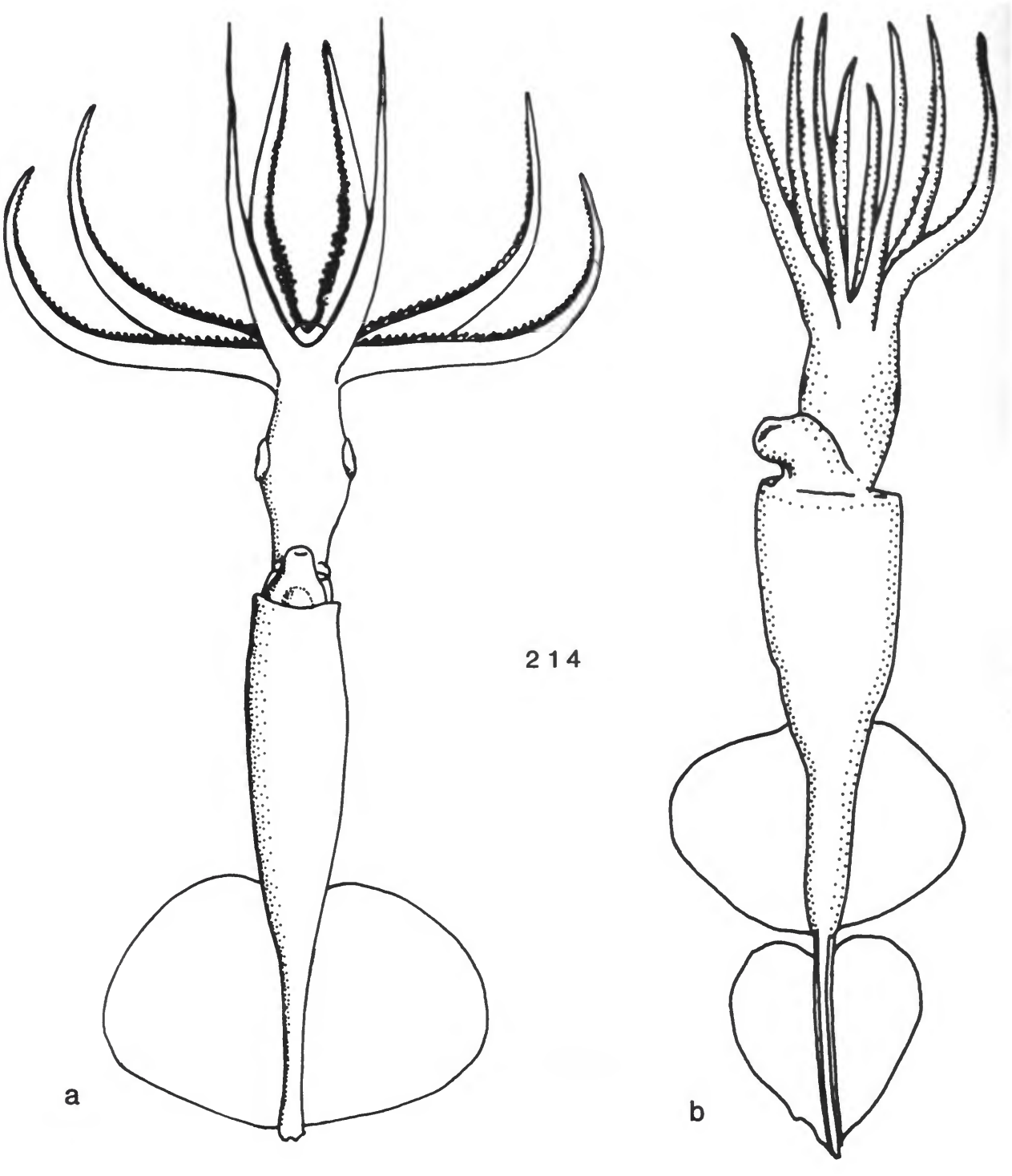

FIGURE 214.—*Grimalditeuthis bonplandi: a,* ventral view, juvenile, 47 mm ML, northeastern Atlantic (original drawing); *b,* ventral view (redrawn from Joubin, 1900).

Family PROMACHOTEUTHIDAE Naef, 1912

(by N.A. Voss)

FAMILY CHARACTERS.—Body texture semisolid, gelatinous; tentacles very thick, muscular; mantle stout, with thick walls, fused to head at nuchal region; fins large, broad, together transversely oval to near-rhomboidal, terminal-lateral; eyes considerably reduced in size; suckers small, arranged in 2 rows on arms; suckers minute, numerous, closely packed in 8 or more rows on club.

REMARKS.—These deep-sea squids are known from only nine specimens (seven recorded in literature) that range in size from a juvenile of 10.5 mm ML to a mature male of 184 mm ML. The family, comprised of one genus and about three species, is widely distributed in North and South Atlantic and Pacific oceans. A revision of the family is in preparation by S. Hess.

Promachoteuthis Hoyle, 1885

GENERIC CHARACTERS.—Family is monogeneric; generic characters are as given for family.

Key to Species* of PROMACHOTEUTHIDAE (Juveniles ~10–17 mm ML)

Fins very large, length about 70% ML, width about 150% ML; arms moderately long, about 80%–100% ML . . . . . ***Promachoteuthis megaptera***

Fins medium to moderately large, length about 25%–40% ML, width about 50%–70% ML; arms short, stout, about 20%–40% ML . . . . . ***Promachoteuthis*** sp. B

* Juvenile not known for *Promachoteuthis* sp. A.

Promachoteuthis megaptera Hoyle, 1885

SPECIES CHARACTERS.—*Young* (Figure 215*a,c*): Fins very large, length approximately 70% ML, width approximately 150% ML; arms moderately long, approximately 80%–100% ML; tentacles moderately long, approximately 150% ML (all characters from holotype; 15 mm ML, approximately 20.7 mm GL).

GEOGRAPHICAL DISTRIBUTION.—Known from only 2 captures in the northwestern Pacific between 31°N to 35°N, and 141°E to 147°E.

VERTICAL DISTRIBUTION.—Closing net captured a 52.4 mm ML female at 2750 m over 6000 m bottom; only other specimen, 15 mm ML (holotype), taken in open bottom trawl at 3431 m.

REFERENCES.—Hoyle (1886), Okutani (1983).

Promachoteuthis sp. A, Toll, 1982

SPECIES CHARACTERS.—*Adults* (Figure 215*d*): Characterized at present only by distinctive gladius taken from complete animal; female, 112 mm ML (93.5 mm GL).

GEOGRAPHICAL DISTRIBUTION.—Single reported specimen from the northeastern Atlantic at ~36°N, 16°W.

VERTICAL DISTRIBUTION.—Captured in open Engel trawl fished at 2650 m during the day.

REFERENCES.—Toll (1982).

Promachoteuthis sp. B, Toll, 1982

SPECIES CHARACTERS.—*Young* (Figures 215*b,e*, 216): 10.5–17.0 mm ML: Fins medium to moderately large, length ~25%–40% ML, width ~50%–70% ML; arms short, stout, ~20%–40% ML; tentacles very stout, ~60%–95% ML.

GEOGRAPHICAL DISTRIBUTION.—Tentatively known only from 4 widely scattered captures in Peru Current between 33°S to 35°S and 72°W to 81°W, and in the Pacific Subantarctic between 56°S to 57°S and 170°E to 73°W.

VERTICAL DISTRIBUTION.—All captures were made with open midwater trawls fished to a maximum depth of between 1463 and 2972 m.

REFERENCES.—Roper and Young (1968, 1975), Toll (1982), S.C. Hess (unpublished data).

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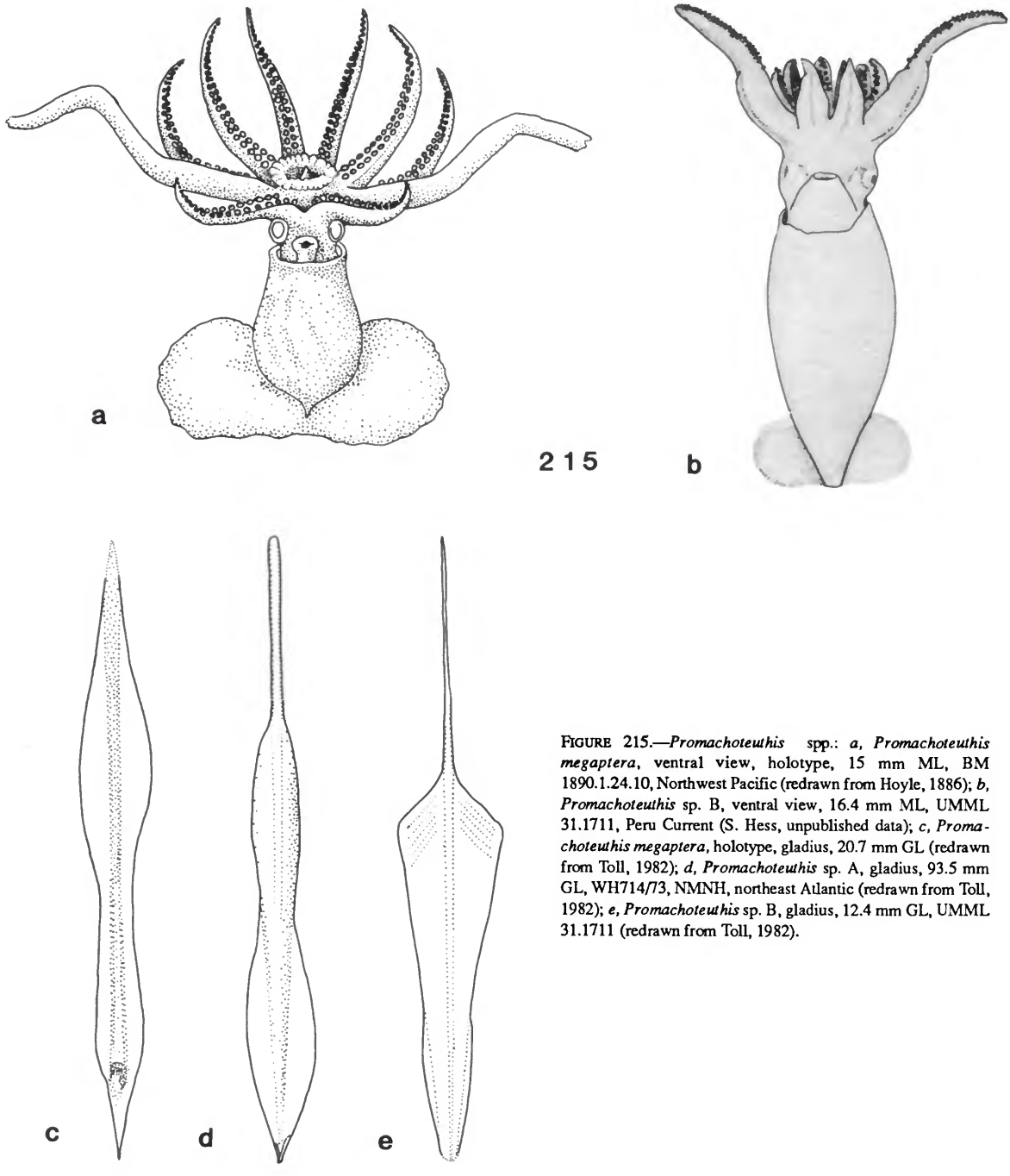

FIGURE 215.—*Promachoteuthis* spp.: *a, Promachoteuthis megaptera*, ventral view, holotype, 15 mm ML, BM 1890.1.24.10, Northwest Pacific (redrawn from Hoyle, 1886); *b, Promachoteuthis* sp. B, ventral view, 16.4 mm ML, UMML 31.1711, Peru Current (S. Hess, unpublished data); *c, Promachoteuthis megaptera*, holotype, gladius, 20.7 mm GL (redrawn from Toll, 1982); *d, Promachoteuthis* sp. A, gladius, 93.5 mm GL, WH714/73, NMNH, northeast Atlantic (redrawn from Toll, 1982); *e, Promachoteuthis* sp. B, gladius, 12.4 mm GL, UMML 31.1711 (redrawn from Toll, 1982).

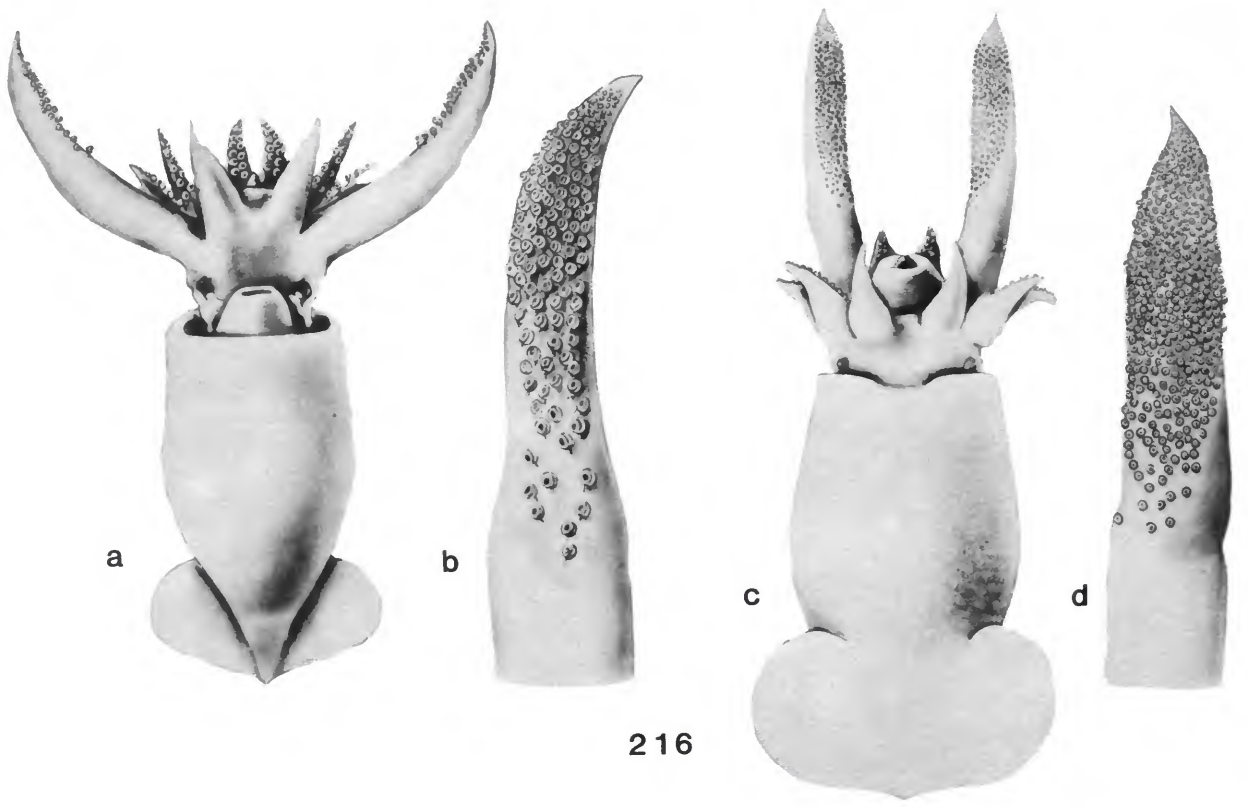

FIGURE 216.—*Promachoteuthis* ? sp. B., Antarctic Ocean: *a*, ventral view, 10.5 mm ML; *b*, tentacular club of same; *c*, dorsal view, 17 mm ML; *d*, tentacular club of same. (From Roper and Young, 1968.)

Family CRANCHIIDAE Prosch, 1849

(by N.A. Voss, S.J. Stephen, and Zh. Dong)

FAMILY CHARACTERS.—Mantle thin-walled, fused to head at nuchal region and to funnel at posterolateral corners; fins vary from separate, small, paddle-shape, subterminal, to medium-large, round, terminal, to ovate or lanceolate, terminal or terminal-lateral; funnel moderately large to very large; head short; eyes small to large with photophores; arms short to medium length, with suckers in 2 rows, except on portions of secondarily modified arms of males; tentacles with 2 rows (except in *Teuthowenia*, with 4 rows) of carpal suckers on major portion of stalks; tentacular club suckers in 4 rows, hooks appear with growth in *Galiteuthis* and *Mesonychoteuthis*.

REMARKS.—Cranchiids occur in large numbers, worldwide in oceanic waters from the Subarctic to the Antarctic, from the surface to unknown depths below 2000 meters. Life history of all species includes early growth in shallow water and ontogenetic descent to deep water where maturation occurs. Cranchiids exhibit varying degrees of diel vertical movement. Two subfamilies, 13 genera, and more than 60 species are known. The majority of the species are undescribed. The family is currently being monographed by N. Voss.

Note: The regions and provinces of the Atlantic referred to in the geographical distribution sections are those of Backus et al. (1977).

Key to Genera of CRANCHIIDAE (Adults)

See N. Voss (1980:374).

Key to Genera of CRANCHIIDAE ("Larvae" and Early Juveniles)

Note: The family (with the exception of *Cranchia* and *Liocranchia*) displays a special "larval" stage characterized by stalked eyes and a short to long arm-crown stalk.

1. Ventral surface of mantle with 1 or 2 cartilaginous strips extending posteriorly from anterior apex of funnel-mantle fusions. Subfamily CRANCHIINAE 2
   Ventral surface of mantle without cartilaginous strips extending posteriorly from anterior apex of funnel-mantle fusions (may have cartilaginous tubercles at points of funnel-mantle fusion, but not in elongate strips). Subfamily TAONIINAE 4
2. Ventral surface of mantle with 2 cartilaginous strips in inverted V-shape pattern extending posteriorly from anterior apex of funnel-mantle fusions (usually not apparent in *Cranchia* < ~10 mm ML); head without arm-crown stalk; eyes sessile 3
   Ventral surface of mantle with one tubercular cartilaginous strip extending posteriorly from anterior apex of funnel-mantle fusion (> ~7 mm ML); head with long arm-crown stalk; eyes stalked . . . . . ***Leachia***
3. Mantle surface with widely or densely set, cross-shape cartilaginous tubercles (> ~4 mm ML) . . . . ***Cranchia***
   Mantle without tubercles except on ventral cartilaginous strips and sometimes on dorsal median line (> ~5 mm ML) . . . . . ***Liocranchia***
4. Funnel-mantle fusion area broad; tubercles absent or barely discernible, straight funnel-mantle fusion cartilage; fins widely separated on rounded posterior end of gladius, or inserted on short rostrum of gladius that projects dorsally free of end of mantle 5
   Funnel-mantle fusion area narrow; tubercles sometimes present on straight, oval, subtriangular, spindle-shape or triangular funnel-mantle fusion cartilages; fins insert on posterolateral margins of blunt or sharp-pointed, diamond-shape lanceola 6
5. Fins widely separated on transversely expanded posterior end of gladius; arm-crown stalk and eye stalks long . . . . . ***Bathothauma***
   Fins inserted on short rostrum of gladius that projects dorsally free of end of mantle; arm-crown stalk and eye stalks short . . . . . ***Helicocranchia***
6. Lanceola broad, diamond-shape with broad, blunt, or pointed end 7
   Lanceola narrow or of medium width, diamond-shape, with narrow, sharp-pointed end 8
7. Lanceola very delicate, with blunt posterior end; eyes oval, with short ventral rostrum; eyes become elliptical in juveniles . . . . . ***Liguriella***
   Lanceola keeled, with long, gradual anterior slope and short, steep posterior slope, posterior end pointed; eyes laterally compressed, with long, pointed, cone-shape ventral rostrum; eyes become tubular in juveniles . . . . . ***Sandalops***
8. Lanceola narrow, with slender gladial spine projecting between fins; terminal portion of tentacles bearing 4 short rows of suckers 9
   Lanceola of medium width, distinctly diamond-shape, with point of gladius, which may project between fins, of medium width; terminal portions of tentacles bearing 4 moderately long to long rows of suckers 11
9. Eye stalks long; arm-crown stalk moderately long; eyes become tubular in juveniles; mantle elongate, slender; arms III longest . . . . . ***Taonius***
   Eye stalks and arm-crown stalk short, stout; mantle stout with posterior taper; arms IV longest 10
10. Funnel-mantle fusion cartilages with 4–6 pointed tubercle complex; nuchal fusion cartilage with single tubercle; forming hooks on midportions of arms seen at > ~45 mm ML. (Antarctic; smallest known "larva" ~15 mm ML) . . . . . ***Mesonychoteuthis***
    Funnel-mantle fusion cartilages with or without tubercles; nuchal fusion cartilage without tubercles, or with multiple tubercles (> ~7 mm ML); hooks not present on arms (Antarctic to Subarctic) . . . . . ***Galiteuthis***

11. Tentacles with 4 rows of carpal suckers except at very base; funnel-mantle fusion cartilages irregularly oval . . . . . ***Teuthowenia***
    Tentacles with 2 rows of carpal suckers except proximal to forming club; funnel-mantle fusion cartilages elongate, triangular 12
12. Mantle moderately stout, sometimes with mucous outer layer; eye stalks long; digestive gland with forming complex photophore (> ~23-30 mm ML) . . . . . ***Megalocranchia***
    Mantle slender; eye stalks medium to short, stout; digestive gland without photophore . . . . . ***Egea***

Subfamily CRANCHIINAE Pfeffer, 1912

Cranchia Leach, 1817

REMARKS.—A single worldwide species currently recognized.

*May be composed of more than one species or subspecies.

Cranchia scabra Leach, 1817 (group)*

SPECIES CHARACTERS.—*Young* (Figure 217*a*): Stout, spindle-shape, often near-round mantle with scattered cross-shape tubercles becoming more numerous with growth (few widely scattered tubercles confined to anterior 1/2 of mantle at ~4-5 mm ML); protruding, but not stalked, small oval eyes; eyes with 14 oval photophores, 7 in outer half circle, 1 midway, and 6 in inner full circle (outer photophores first seen at ~10 mm ML, inner photophores at ~15-17 mm ML); small, separate, paddle-shape fins gradually become round and unite posteriorly with growth; short, nontubercular, inverted V-shape cartilaginous strips usually not apparent until ~10-15 mm ML.

GEOGRAPHICAL DISTRIBUTION.—Circumglobal in tropical and subtropical waters; distribution generally described by north and south subtropical convergences.

VERTICAL DISTRIBUTION.—Juveniles present in upper 400 m day and night. There is a tendency for larger juveniles to extend range into deeper water. Adults have been taken in open nets fished at depths of 1900-2000 m.

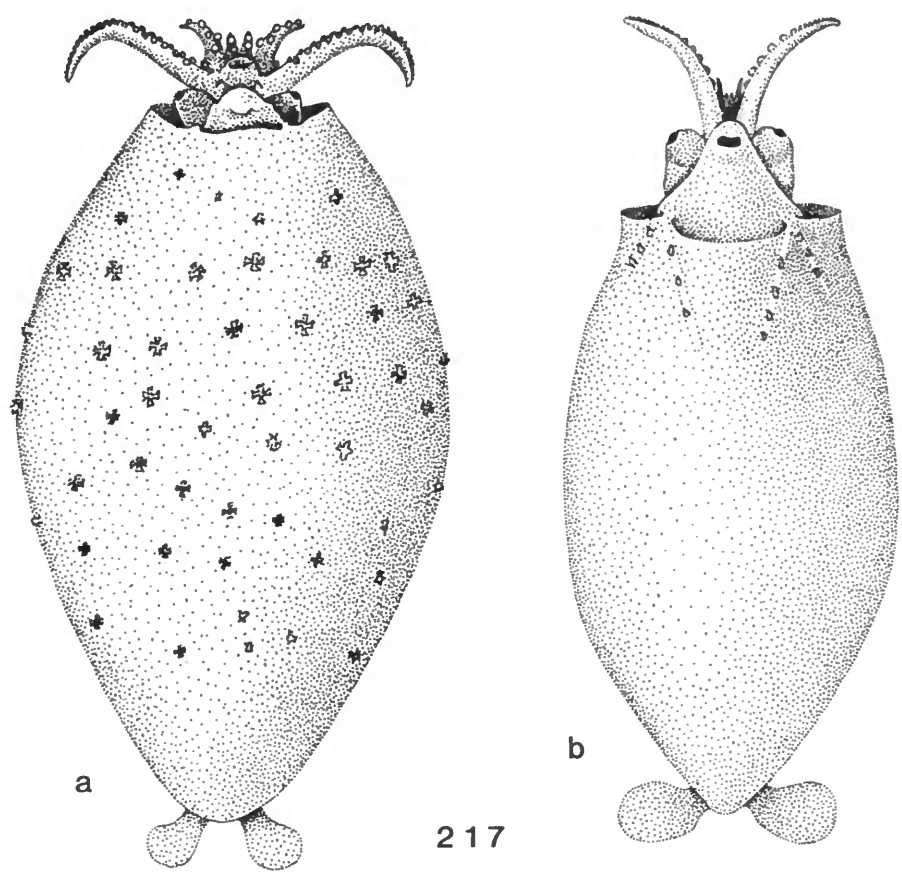

FIGURE 217.—*a, Cranchia scabra*, ventral view, North Atlantic, 8 mm ML; *b, Liocranchia reinhardtii*, ventral view, North Atlantic, 6 mm ML (both from N. Voss, 1980).

REFERENCES.—Chun (1910), Lu and Clarke (1975b), Clarke and Lu (1975), N. Voss (1980, unpublished data).

Liocranchia Pfeffer, 1884

GENERIC CHARACTERS.—*Young:* Stout, spindle-shape mantle; inverted V-shape, moderately long, tubercular cartilaginous strips at each funnel-mantle fusion point; protruding, but not stalked, small, oval eyes with 4 or more round to oval photophores; small, separate, paddle-shape fins, gradually become round and unite posteriorly with growth.

REMARKS.—At present, two widely distributed species are recognized.

Liocranchia reinhardtii (Steenstrup, 1856) (group)*

SPECIES CHARACTERS.—*Young* (Figure 217*b*): Ventral tubercular strips approximately co-equal in length (tubercles first seen at ~5–6 mm ML); median dorsal lines with tubercles (tubercles first seen at ~8 mm ML); eyes with 14 photophores, 7 in outer half circle, 1 midway, and 6 in inner full circle (outer photophores first seen at ~8 mm ML, inner photophores at ~12 mm ML).

GEOGRAPHICAL DISTRIBUTION.—Circumglobal in tropical and subtropical waters; distribution generally described by north and south subtropical convergences.

VERTICAL DISTRIBUTION.—Juveniles concentrated in upper few hundred meters; older animals seek greater depths, with adults extending to below 1000 m. Using open-closing gear, captures of "larvae" < ~6 mm ML below 200 m and of an apparently spent female at 775 m suggest that spawning and hatching occur in deep midwater.

REFERENCES.—Chun (1910), Lu and Clarke (1975a,b), Clarke and Lu (1975), Young (1978), N. Voss (1980, unpublished data).

Liocranchia valdiviae Chun, 1906

SPECIES CHARACTERS.—*Young:* Ventral tubercular strips of unequal length, ventralmost strips clearly the longest (usually apparent at ~10–15 mm ML); median dorsal line without tubercles; eyes with 4 photophores in half circle on ventral surface (first seen at ~9 mm ML).

GEOGRAPHICAL DISTRIBUTION.—Primarily confined to tropical and equatorial waters of Pacific and Indian oceans; occurs in the southeastern Atlantic in the area of the Benguela Current where both juveniles and adults have been captured.

VERTICAL DISTRIBUTION.—Young of ~5–15 mm ML are concentrated in upper few hundred meters; juveniles >15 mm to ~25 mm ML in depth of ~500–700 m; animals > ~25 mm ML in progressively greater depths to in excess of 1000 m.

REMARKS.—Young of < ~8 mm ML are difficult to distinguish from the co-occuring *L. reinhardtii*.

*May be composed of more than one species or subspecies.

REFERENCES.—Chun (1910), Roper and Young (1975), Young (1978), N. Voss (1980, unpublished data).

Leachia Lesueur, 1821

GENERIC CHARACTERS.—*Young:* Moderately stout, spindle-shape mantle elongates with growth; single, tubercular cartilaginous strip extends from each funnel-mantle fusion point; head with long, narrow arm-crown stalk; arms III become disproportionately elongate early in growth; eyes with 5–21 round to oval photophores, on long stalks; stout, solid gladial spine projects between transversely elliptical fins.

Note: Photophore pattern on eyes, and detail of tubercular strips on ventral surface of mantle are prime features for specific identification.

GEOGRAPHICAL DISTRIBUTION.—Genus occurs circumglobally in tropical and subtropical waters.

REMARKS.—Ongoing studies (N. Voss) indicate that the genus is composed of approximately 11 closely related species whose geographic distributions are usually contiguous, but considerable overlaps may occur. Of the 14 nominal species, 6 appear to be valid. Genus displays an extended "larval" stage; eyes become sessile between about 40–105 mm ML. There is a tendency of largest maturing species to occur in areas of high productivity and "dwarf" species to occur in low productive central waters of gyres. Distributions of individual species are relatively restricted.

Leachia lemur (Berry, 1920)

SPECIES CHARACTERS.—*Young* (Figure 219*a*): Eyes with 5 photophores, 4 outer (seen at ~24 mm ML), 1 inner (> ~26 mm ML); tubercular strips with multifid tubercles relatively simple, usually 3–4 pointed.

GEOGRAPHICAL DISTRIBUTION.—Primarily restricted to North Atlantic Subtropical Region west of about 50°W (North and South Sargasso seas).

VERTICAL DISTRIBUTION.—Juveniles concentrated in upper few hundred meters; larger animals progressively seek deeper depths to >1000 m. Appears to mate and spawn in deep water.

REMARKS.—A small maturing species (males and females mature at ~60–70 mm ML).

REFERENCES.—N. Voss (unpublished data).

Leachia atlantica (Degner, 1925) (group)*

SPECIES CHARACTERS.—*Young* (Figure 218*a,b*, 219*b*): Eyes with 6 (occasionally 5) photophores, 5 (occasionally 4) outer, 1 inner (3 outer, 1 inner seen at ~32 mm ML; full pattern seen at > ~50 mm ML); tubercular strips with ~7–8 large, multifid, rosette-shape tubercles with intervening small tubercles.

GEOGRAPHICAL DISTRIBUTION.—North Atlantic Subtropical Region, Gulf of Mexico, Straits of Florida, and northern Caribbean.

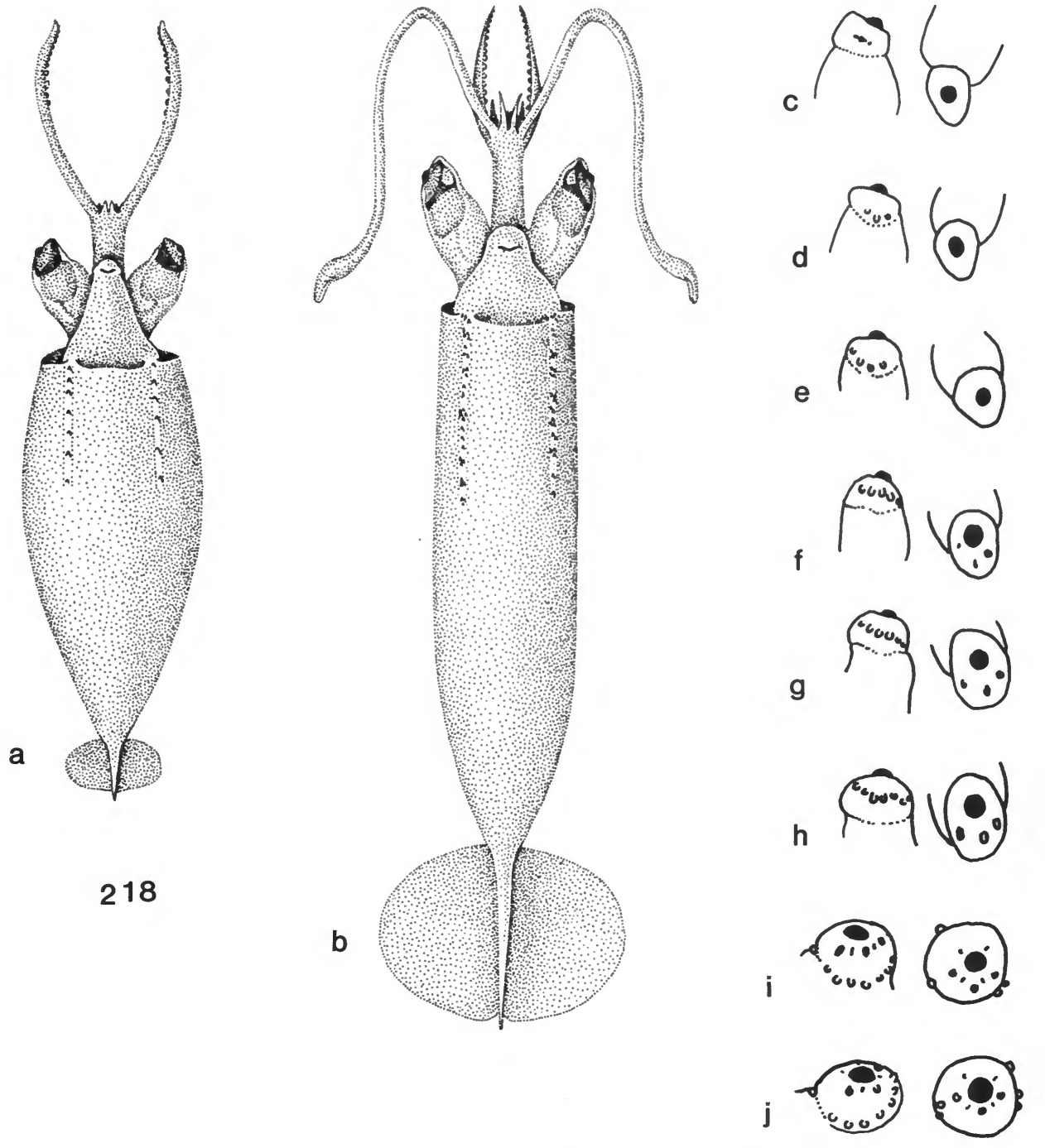

FIGURE 218.—*a,b, Leachia atlantica*, Gulf of Mexico: *a*, ventral view, 8 mm ML; *b*, ventral view, 32 mm ML (both from N. Voss, 1980). *c–j, Leachia dislocata*, development of eye photophores, lateral and ventral views, California Current: *c*, 16 mm ML; *d*, 22 mm ML; *e*, 25 mm ML; *f*, 35 mm ML; *g*, 44 mm ML; *h*, 64 mm ML; *i*, 125 mm ML; *j*, 143 mm ML (all redrawn from Young, 1972a).

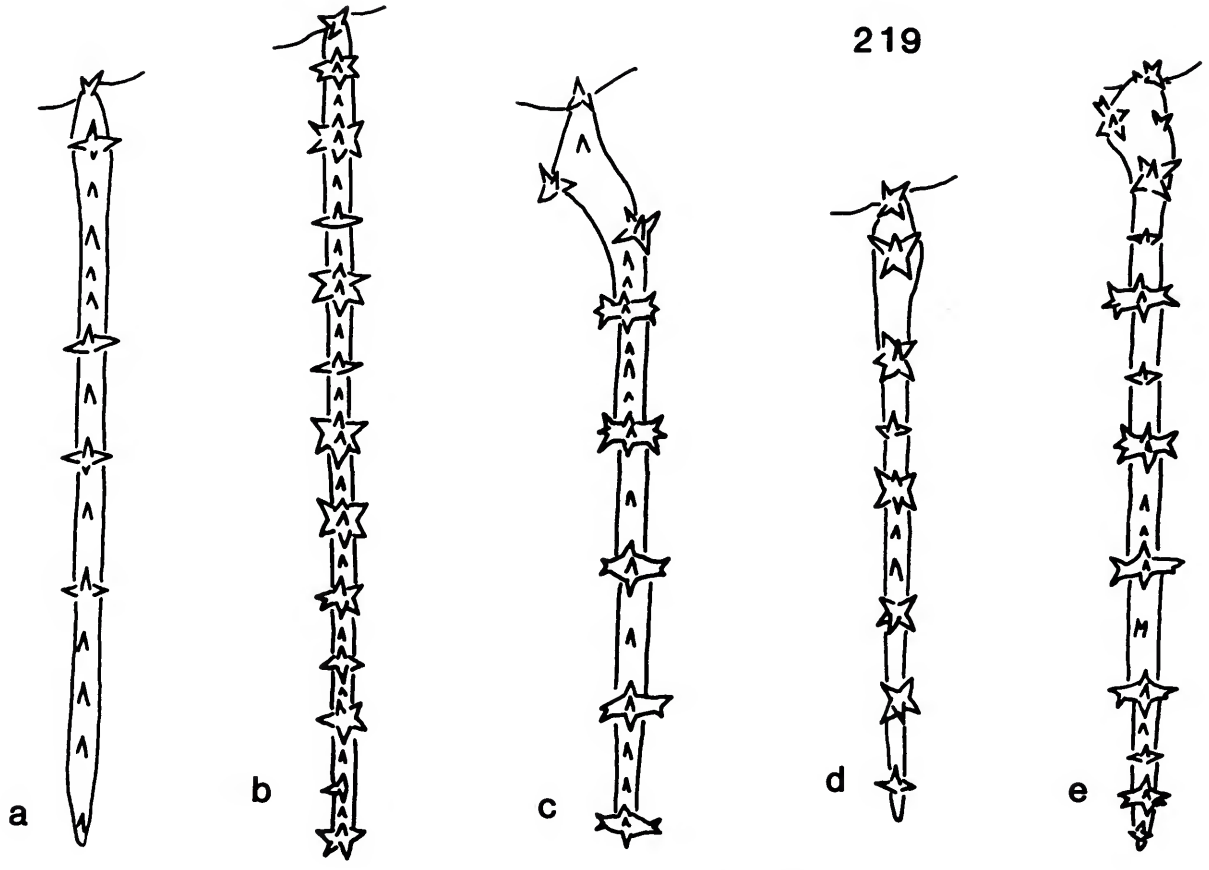

FIGURE 219.—*a–e*, Left ventral tubercular strips: *a*, *Leachia lemur*, North Sargasso Sea, Discovery 8281-11, 42 mm ML; *b*, *Leachia atlantica*, North Atlantic subtropical, Dana 1367-V, 54 mm ML; *c*, *Leachia dislocata*, California Current, MV 66-I-10, 34 mm ML; *d*, *Leachia danae*, eastern tropical Pacific, TO 5801-17, 53 mm ML; *e*, *Leachia ? pacifica*, Hawaiian waters, FIDO VI, 41 mm ML. (All original drawings.)

VERTICAL DISTRIBUTION.—Juveniles concentrated in upper few hundred meters; larger animals seek progressively greater depths to >1000 m. There is evidence of some diel vertical movement. Numerous night and early morning captures of mature and spent females at the surface indicate that spawning occurs in surface waters.

REMARKS.—Co-occurs with *L. lemur* in western Atlantic subtropical waters.

REFERENCES.—Degner (1925), N. Voss (unpublished data).

Leachia dislocata Young, 1972 (group)*

SPECIES CHARACTERS.—*Young* (Figure 218*c–j*, 219*c*): Eyes with 15 photophores, 8 outer, 7 inner (see figure for approximate times of first appearance); tubercular strips with second large, anterior tubercle noticeably displaced from remainder of line (clearly seen at ~15 mm ML); large, multifid tubercles more transversely elongate than round.

GEOGRAPHICAL DISTRIBUTION.—Eastern Pacific in California Current between ~25°N and 45°N, west to ~160°W, and in Peru-Chile Current between ~15°S and 25°S.

VERTICAL DISTRIBUTION.—Juveniles concentrated in upper few hundred meters; larger animals seek progressively greater depths to >1000 m. Diel vertical migration occurs in at least part of the population. Captures at night of mature males in the upper 200 m and a spent female at the surface suggest that mating and spawning occur in shallow water.

REFERENCES.—Young (1972a), N. Voss (unpublished data).

*May be composed of more than one species or subspecies.

Leachia danae (Joubin, 1931)

SPECIES CHARACTERS.—*Young* (Figure 219*d*): Eyes with 21 photophores, 8 outer, 5 middle, 8 inner (6 outer, 5 middle seen at ~38 mm ML; full pattern at ~71 mm ML); suckers on middle of arms III with single, large central tooth (first seen forming at ~55-60 mm ML); tubercular strips with no noticeably displaced tubercles; large, multifid tubercles round.

GEOGRAPHICAL DISTRIBUTION.—Eastern Pacific, in equatorial waters between ~14°S and 23°N, west to ~145°W.

VERTICAL DISTRIBUTION.—Small juveniles concentrated in upper few hundred meters; with growth, animals seek progressively greater depths to >1000 m. Some diel vertical movement occurs.

REMARKS.—At maturity, this is the largest species in the genus (males, ~150-183 mm ML).

REFERENCES.—N. Voss (unpublished data).

Leachia ? pacifica (Issel, 1908) (group)*

SPECIES CHARACTERS.—*Young* (Figure 219*e*): Eyes with 6 photophores, 5 outer, 1 inner (4 outer, 1 inner seen at ~39 mm ML; full pattern at ~50 mm ML); tubercular strips with second, large, anterior tubercle noticeably displaced from remainder of line (clearly seen at ~15-18 mm ML); large, multifid tubercles more transversely elongate than round.

GEOGRAPHICAL DISTRIBUTION.—Tropical waters of North Pacific, Indo-Pacific, and equatorial waters of Indian Ocean.

VERTICAL DISTRIBUTION.—Juveniles to ~35 mm ML concentrated in upper 200 m; larger animals found throughout water column from ~200 m to at least 1800 m. Maturation occurs in the greater depths.

REMARKS.—Species matures at a small size (~55-60 mm ML). The species co-occurs in the central North Pacific with *L. dislocata,* and in the Indian Ocean with a closely related, undescribed congener. Small "larvae" of the three species are difficult to separate.

REFERENCES.—Young (1975b, 1978), N. Voss (unpublished data).

Subfamily TAONIINAE Pfeffer, 1912

Helicocranchia Massy, 1907

GENERIC CHARACTERS.—*Young:* Mantle elongate, cylindrical, often with mucous outer layer; funnel very large (apparent as small as 2.5 mm ML); eyes oval, with pronounced ventral rostrum, on short, stout stalks; head with short arm-crown stalk; fins small, paddle-shape, inserted on posterior tip (rostrum) of gladius that projects dorsally free of end of mantle.

Note: Distinctive shape of posterior end of gladius, chromatophore pattern, and patterns of sucker enlargement on arms and clubs are often useful features for separating species.

REMARKS.—Genus, currently being revised by N. Voss, is composed of about 14 species, the majority are undescribed. Co-occurence of congeners is common over the range of the genus in tropical, subtropical, and North Atlantic temperate waters.

Helicocranchia pfefferi Massy, 1907

SPECIES CHARACTERS.—*Young* (Figure 220): Gladius with elongate, narrow posterior rostrum; funnel organ with L-shape ventral pads, posterior portions shorter and stouter than anterior portions (seen at ~6 mm ML); no suckers disproportionately enlarged on arms III or on tentacular club; tentacles moderately long and robust, <100% ML.

GEOGRAPHICAL DISTRIBUTION.—Widespread in North Atlantic Temperate Region.

VERTICAL DISTRIBUTION.—"Larvae" and small juveniles concentrated in approximately upper 300 m; vertical range increases with growth; maturation occurs in deep water to at least 2000 m. Some diel vertical movement is suggested. Captures of 4 mm ML "larvae" in near-surface waters and of mated and spent females at the surface indicate that at least some spawning occurs in shallow water.

REFERENCE.—N. Voss (unpublished data).

Helicocranchia beebei Robson, 1948 (group)†

SPECIES CHARACTERS.—*Young* (Figure 221): "Larvae" and juveniles are very difficult, and often impossible, to separate from *H. pfefferi* except by geographic occurrence.

GEOGRAPHICAL DISTRIBUTION.—Eastern tropical Pacific; California Current north to ~34°N; Peru-Chile Current south to ~20°S.

VERTICAL DISTRIBUTION.—Larvae of 6-9 mm ML have been taken between 100 and 300 m. Larger young to ~40 mm ML are concentrated between 200 and 400 m. With subsequent growth, animals tend to occur in deeper water. Near-mature and mature males have been taken in open nets fishing to between 1000 and ~2200 m. There is no evidence of diel vertical migration.

REFERENCES.—Nesis (1973a; reported as *H. pfefferi*), Roper and Young (1975; reported as *H. pfefferi*), N. Voss (unpublished data).

Helicocranchia papillata (G. Voss, 1960)

SPECIES CHARACTERS.—*Young* (Figure 222): Gladius with short, stout posterior rostrum; funnel organ with crescentic, elongate, oval ventral pads; arms III with enlarged suckers on median portions (first seen at ~7 mm ML); tentacular club with ventral row of suckers enlarged; tentacles long, narrow, usually >100% of ML in larvae >10 mm ML.

*May be composed of more than one species or subspecies.

†May be composed of more than one subspecies.

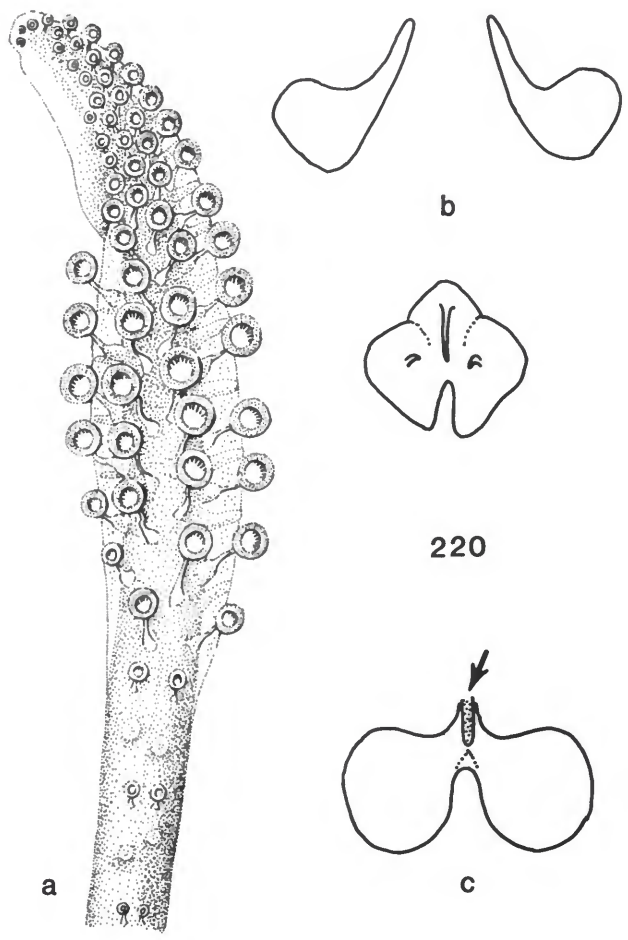

FIGURE 220.—*Helicocranchia pfefferi*, North Atlantic: *a*, left tentacular club, Dana 4158 XVI, 45 mm ML; *b*, funnel organ, Dana 4149 IV, 17 mm ML; *c*, ventral view of posterior end of same, showing projecting, elongate, narrow rostrum of gladius (*a*, C. McSweeny, unpublished data; *b,c*, original drawings).

GEOGRAPHICAL DISTRIBUTION.—Widespread in North Atlantic Subtropical Region, Carribbean, and Gulf of Mexico.

VERTICAL DISTRIBUTION.—"Larvae" and juveniles concentrated in upper 300 m; vertical range of juveniles appears to increase with growth; maturation occurs in deep waters to >2000 m. Captures of "larvae" <4 mm ML and near-spent females in upper 100 m indicate that at least some spawning occurs in shallow water.

REFERENCES.—Clarke and Lu (1974; reported as *H. pfefferi*), N. Voss (unpublished data).

Bathothauma Chun, 1906

GENERIC CHARACTERS.—*Young* (Figure 223): Mantle elongate, sac-shape, rounded posteriorly; fins small, paddle-shape, widely set on transversely expanded, posterior end of gladius; head with long arm-crown stalk; eyes oval, with ventral rostrum, on long stalks; tentacles stout in early "larvae," to long narrow in late "larvae" and juveniles, with distal portions markedly stouter than proximal portions.

Note: "Larvae" and juveniles are very difficult to identify to species. At present only subadult and adult males can be confidently separated.

GEOGRAPHICAL DISTRIBUTION.—Genus occurs circumglobally in tropical and subtropical waters (with exception of apparent absence in South Atlantic Subtropical), and extends into temperate waters in northeastern Atlantic and in South Pacific.

REMARKS.—Ongoing studies (N. Voss) indicate that genus is composed of about four closely related species. Genus displays an extended "larval" stage; eyes become sessile between about 80–150 mm ML. Mantle lengths are difficult to determine because of tendency for mantle to greatly contract on preservation. Contiguous geographic distributions of congeners are typical of genus.

Bathothauma lyromma Chun, 1906

SPECIES CHARACTERS.—See "Note" above. At present, only subadult and adult males can be confidently separated.

GEOGRAPHICAL DISTRIBUTION.—Atlantic Tropical and North Subtropical regions; extends into temperate waters to ~45°N in northeastern Atlantic.

VERTICAL DISTRIBUTION.—Young to ~40 mm ML concentrated between ~100 to 300 m; with growth, animals seek progressively greater depths to >1500 m. Maturation and mating occur in deep midwaters. There is no evidence of diel vertical migration.

REFERENCES.—Aldred (1974; specimens from Indian Ocean not of this species), Clarke and Lu (1975), N. Voss (unpublished data).

Sandalops Chun, 1906

GENERIC CHARACTERS.—*Young* (Figure 224): Mantle elongate, cylindrical; fins small, inserted on distinctive broad, diamond-shape lanceola; lanceola with distinct, median dorsal keel; broad, pointed posterior end of gladius projects between fins; head with short, stout arm-crown stalk; eyes markedly laterally compressed, with long, pointed, cone-shape ventral rostrum, on moderately long stalks; eyes tubular in juvenile; tentacles long, narrow.

Note: At present, only subadults and adults can be confidently identified to species.

GEOGRAPHICAL DISTRIBUTION.—Genus occurs circumglobally in tropical and subtropical waters.

REMARKS.—Ongoing studies (N. Voss) indicate that genus is composed of 3–4 closely related species.

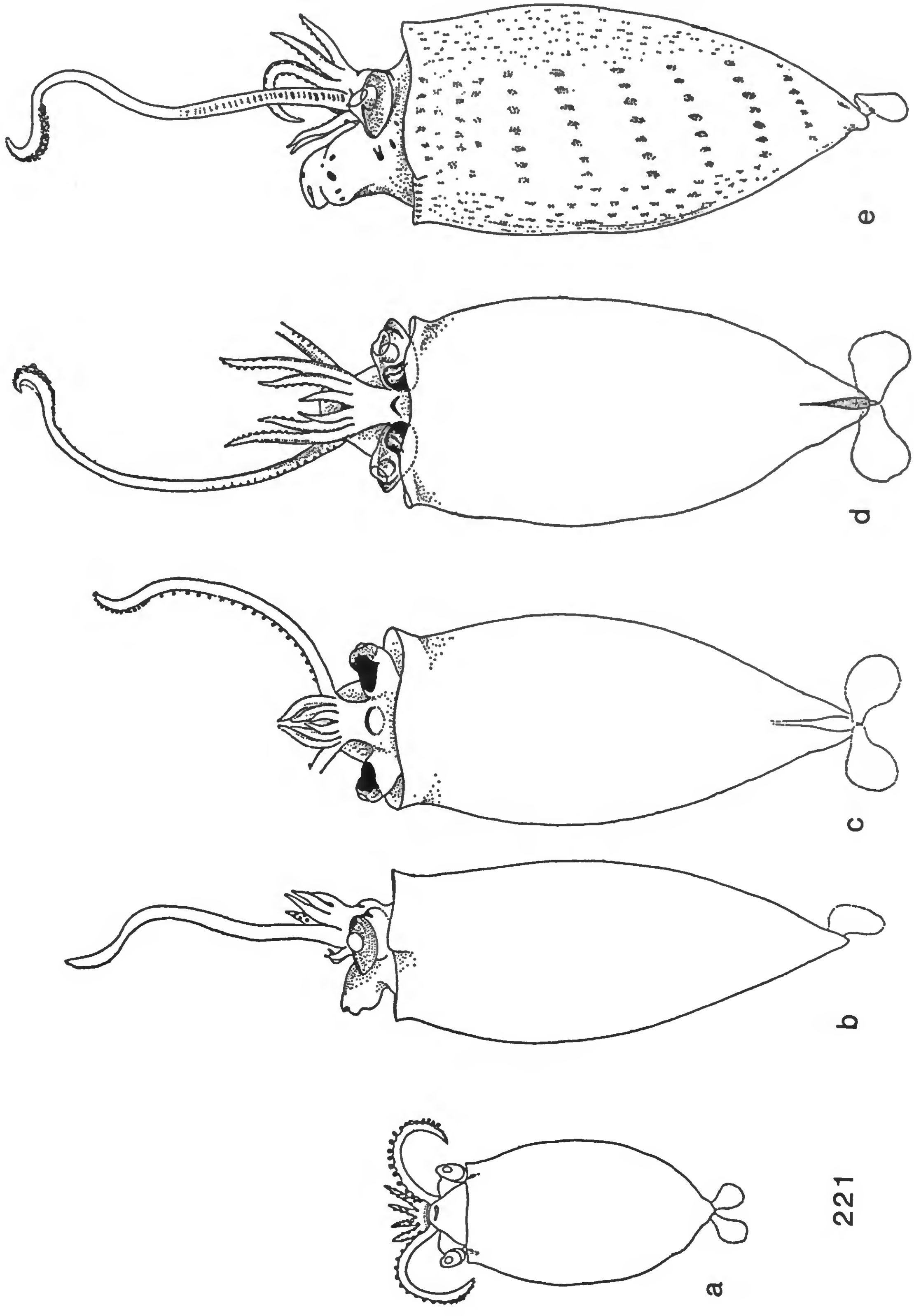

FIGURE 221.—*Helicocranchia beebei*, California Current: *a*, ventral view, ~5 mm ML; *b,c*, dorsal and lateral views, ~8 mm ML; *d,e*, dorsal and lateral views, ~22 mm ML (*e* shows characteristic chromatophore pattern). (From Okutani and McGowan, 1969.)

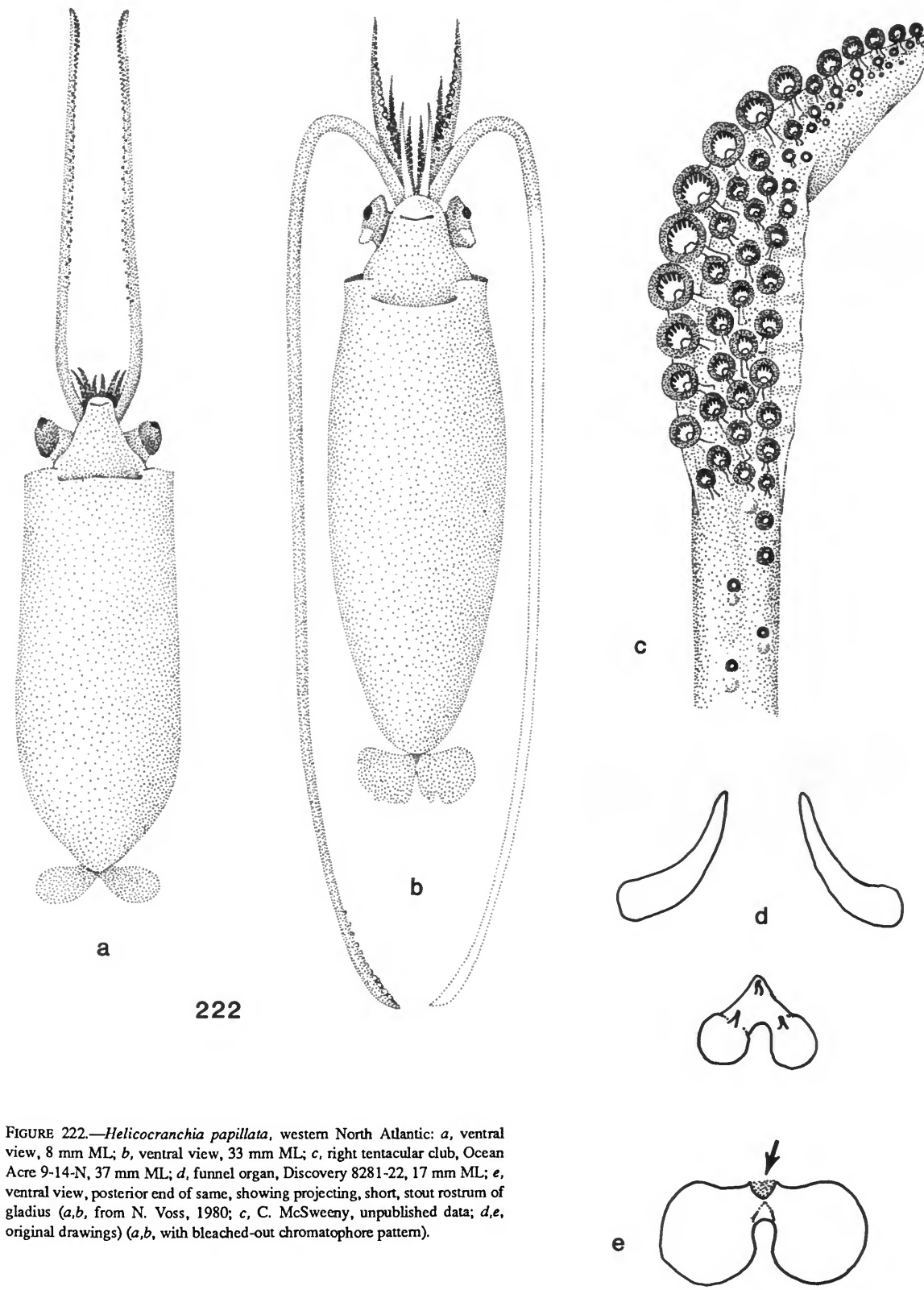

FIGURE 222.—*Helicocranchia papillata*, western North Atlantic: *a*, ventral view, 8 mm ML; *b*, ventral view, 33 mm ML; *c*, right tentacular club, Ocean Acre 9-14-N, 37 mm ML; *d*, funnel organ, Discovery 8281-22, 17 mm ML; *e*, ventral view, posterior end of same, showing projecting, short, stout rostrum of gladius (*a,b*, from N. Voss, 1980; *c*, C. McSweeny, unpublished data; *d,e*, original drawings) (*a,b*, with bleached-out chromatophore pattern).

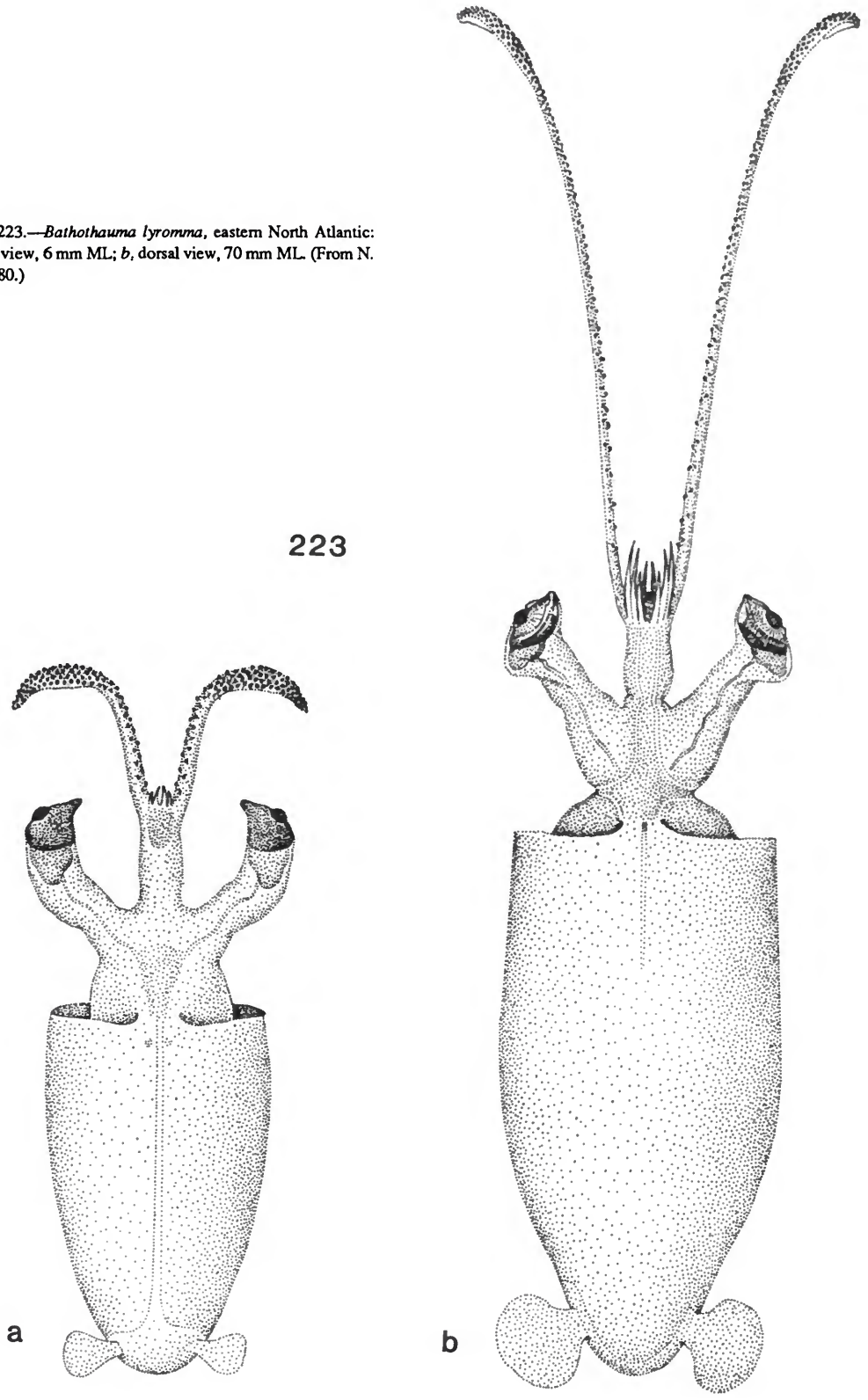

FIGURE 223.—*Bathothauma lyromma*, eastern North Atlantic: *a*. dorsal view, 6 mm ML; *b*, dorsal view, 70 mm ML. (From N. Voss, 1980.)

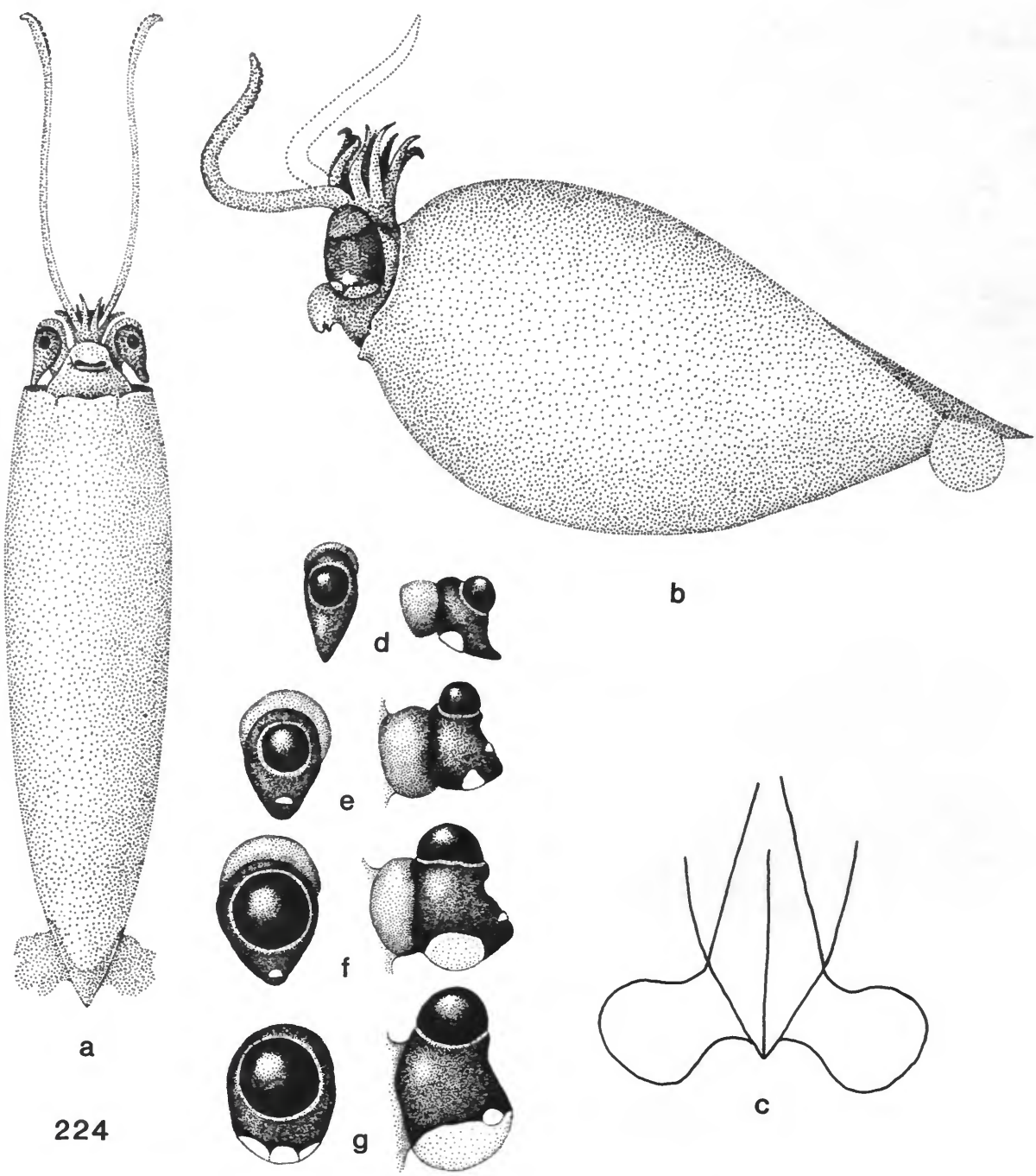

FIGURE 224.—*Sandalops* sp.: *a*, ventral view, Indo-West Pacific, 24 mm ML; *b*, lateral view, central North Pacific, juvenile, 42 mm ML (*a,b*, from N. Voss, 1980). *c*, *Sandalops melancholicus*, dorsal view of posterior end, southwest Indian Ocean, 16 mm ML (original drawing). *d–g*, *Sandalops* sp., ontogenetic series showing changes in shape of eye and development of ocular photophores; anterior and ventrolateral views of left eye, central Pacific: *d*, 27 mm ML; *e*, 26 mm ML; *f*, 33 mm ML; *g*, 38 mm ML (*d–g*, from Voss and Voss, 1983).

Sandalops melancholicus Chun, 1906 (group)*

SPECIES CHARACTERS.—At present, only subadults and adults can be confidently identified to species.

GEOGRAPHICAL DISTRIBUTION.—Tropical and subtropical regions of Atlantic; Indian Ocean from ~10°N south to Subtropical Convergence.

VERTICAL DISTRIBUTION.—"Larvae" to ~30 mm ML concentrated in upper few hundred meters; with growth, animals seek progressively greater depths to >2000 m. Maturation and mating occur in deep water. There is no evidence of diel vertical migration.

REFERENCES.—Nesis (1974a (specimens east of 120°E in Indo-West Pacific probably not of this species-group), 1974b), N. Voss (unpublished data).

Liguriella Issel, 1908

GENERIC CHARACTERS.—*Young* (Figure 225): Mantle stout, spindle-shape; fins paddle-shape in "larvae" <~15 mm ML, become oval with growth and insert on delicate, posteriorly blunt-pointed, moderately broad, diamond-shape lanceola; head with medium to long arm-crown stalk; eyes oval, with short ventral rostrum, on long stalks (< ~15 mm ML); tentacles moderately long, usually stout in "larvae" < ~15 mm ML, with distal portions heavier than proximal, 4 rows of suckers on distal 1/3–3/4, depending on state of contraction; funnel-mantle fusion cartilages irregularly oval, with 2 small tubercles at anterior ends in juveniles > ~30 mm ML.

GEOGRAPHICAL DISTRIBUTION.—Genus occurs circumglobally in tropical and subtropical waters, and possibly in Southern Subtropical Convergence.

REMARKS.—Ongoing studies (N. Voss) indicate that genus is composed of two or more species. Genus is poorly represented in collections, and has not been studied in sufficient detail to clearly separate species. At present, a single cosmopolitan species is recognized.

Liguriella podophtalma Issel, 1908 (group)*

SPECIES CHARACTERS.—At present, only subadults and adults can be confidently identified to species.

VERTICAL DISTRIBUTION.—"Larvae" and juveniles to ~40 mm ML concentrated between subsurface and ~400 m; with growth, animals seek progressively greater depths. Largest known individual, a subadult of 243 mm ML, was captured in an open net fished to ~1500 m. Some diel vertical movement appears to occur.

REFERENCES.—Nesis (1974a; in part), N. Voss (1980, unpublished data).

*Composed of more than one species.

Taonius Steenstrup, 1861

GENERIC CHARACTERS.—*Young:* Mantle elongate, narrow, cone-shape; fins paddle-shape in "larvae" < ~18 mm ML, inserted on elongate, diamond-shape lanceola; fins and posterior end of gladius elongate early with growth (at ~20 mm ML fins are short, lanceolate, and inserted on short, narrow pseudoconus; by ~45 mm ML fins are long, lanceolate, inserted on long, narrow pseudoconus); head with moderately long arm-crown stalk; eyes elliptical to oval, on long stalks in "larvae" < ~22 mm ML; with growth, eyes become tubular in juvenile, with large tripartite-appearing photophore on posteroventral surface; suckers of club manus with 1 or 2 large, central, hook-like teeth first seen forming on rings of median suckers in juveniles of ~50–60 mm ML.

Note: "Larvae" and small juveniles are difficult to identify to species. Proportional length of gladial tail (terminal portion of gladius projecting beyond expanded fins) and dentition pattern, or lack of dentition, on midarm suckers are helpful features in separating juveniles of some species.

GEOGRAPHICAL DISTRIBUTION.—Genus occurs circumglobally in tropical, subtropical, temperate, and subpolar regions.

REMARKS.—Ongoing studies (N. Voss) indicate that the genus is composed of about five closely related species. The long-stalked-eye "larval" stage, spent in shallow water, is brief. Contiguous geographic distributions of congeners are typical of the genus.

Taonius pavo (Lesueur, 1821)

SPECIES CHARACTERS.—*Young* (Figure 226): Gladial tail long in juveniles; midarm suckers on arms II and III with low teeth on distal margins.

GEOGRAPHICAL DISTRIBUTION.—Species is widely distributed in Atlantic between ~45°N to possibly the Southern Subtropical Convergence, and may extend into the western Indian Ocean in the area of the Agulhas Current.

VERTICAL DISTRIBUTION.—Long-stalked-eye "larvae" concentrated in surface 200 m; juveniles of ~25–50 mm ML concentrated between ~400 and 600 m; larger juveniles, with growth, progressively extend range to greater depths. Maturation occurs in deep water to at least 2000 m. Captures of mature females at the surface at night indicate that spawning occurs in shallow water. There is no evidence for diel vertical migration, but subadults appear to range widely in water column.

REFERENCES.—Clarke and Lu (1974, 1975; reported as *Galiteuthis triluminosa*), Roper and Young (1975); Lu and Roper (1979), N. Voss (unpublished data).

Taonius borealis (Nesis, 1972)

SPECIES CHARACTERS.—*Young:* Gladial tail relatively short; midarm suckers on arms II and III with numerous low

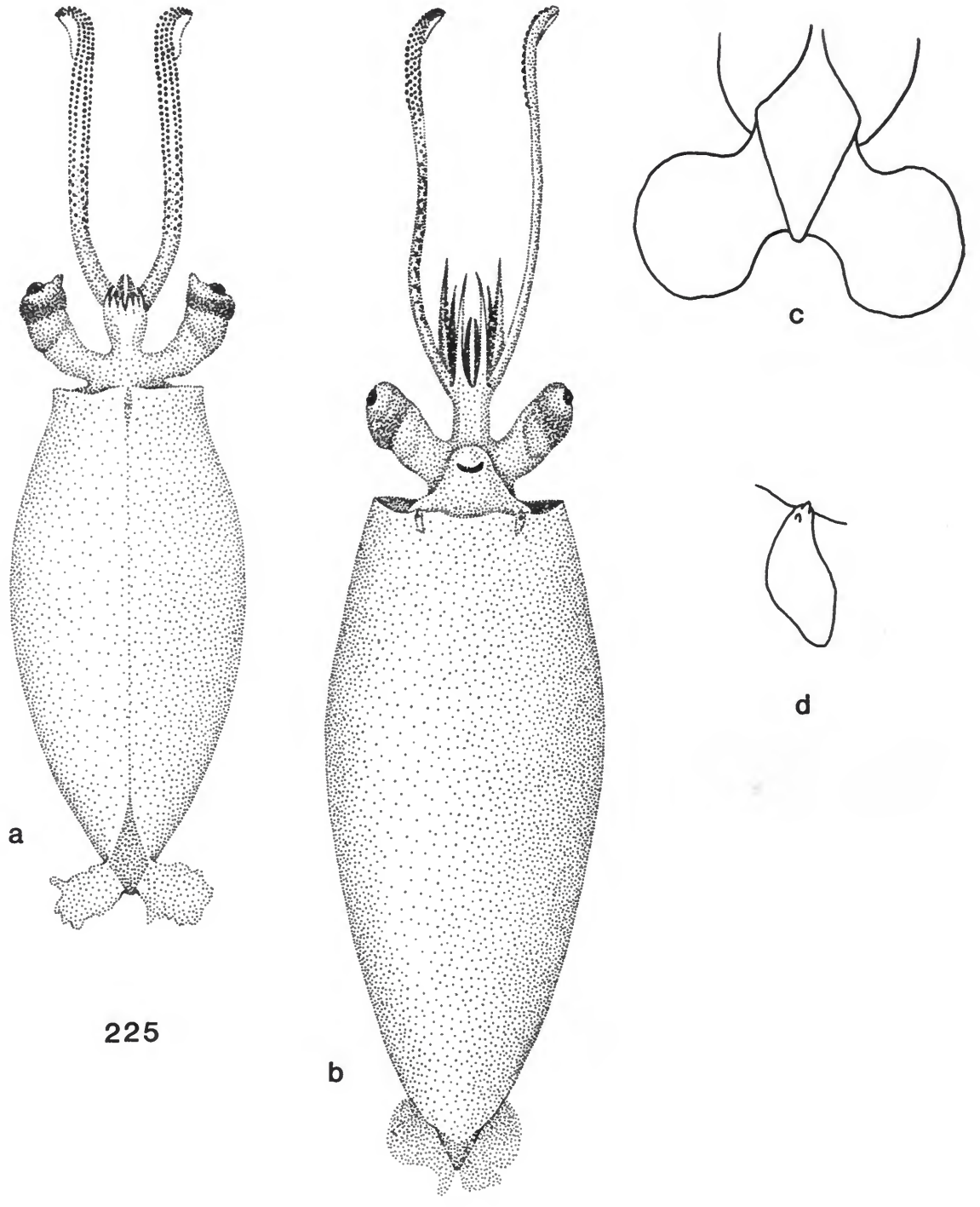

FIGURE 225.—*Liguriella podophtalma*, South Atlantic and southwestern Indian Ocean: *a*, dorsal view, 12 mm ML; *b*, ventral view, 68 mm ML; *c*, dorsal view of posterior end, SAM SM 45, 14 mm ML; *d*, right funnel-mantle fusion cartilage, AB(6)339-A7228, 35 mm ML (*a,b*, from N. Voss, 1980; *c,d*, original drawings).

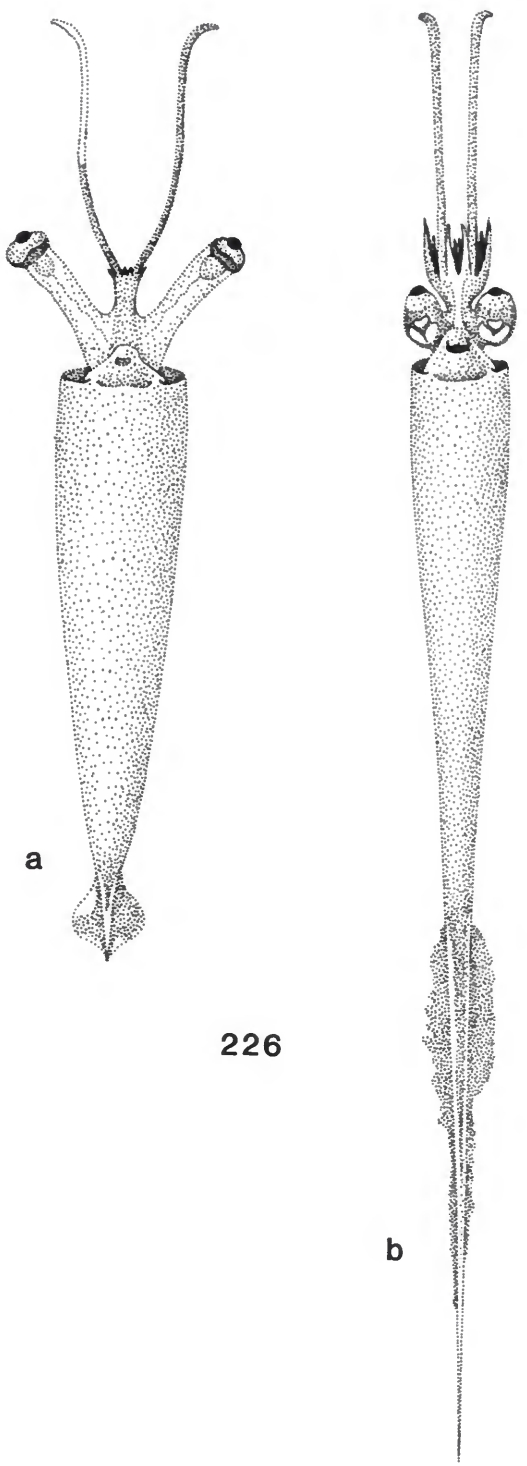

FIGURE 226.—*Taonius pavo*, North Atlantic: *a*, ventral view, 20 mm ML; *b*, ventral view, 80 mm ML. (From N. Voss, 1980.)

teeth around entire margins.

GEOGRAPHICAL DISTRIBUTION.—Pacific Subarctic.

VERTICAL DISTRIBUTION.—"Larvae" occur in upper 200 m; small juveniles concentrated between ~400 to 600 m, and progressively increase depth range with growth. Maturity occurs in deep water to >2000 m. Some diel vertical movement appears to occur.

REFERENCES.—Nesis (1972; reported as *Belonella pacifica borealis*), N. Voss (unpublished data).

Galiteuthis Joubin, 1898

GENERIC CHARACTERS.—*Young:* Mantle moderately stout, spindle-shape; fins small, paddle-shape at < ~15 mm ML, change with growth to lanceolate with intervening stout, gladial spine; head with short to medium length arm-crown stalk; eyes oval, without ventral rostrum, on stout, short to medium length stalks in "larvae"; club manus with median suckers changing into hooks (first seen at ~35–60 mm ML); arms IV typically the longest.

Note: Pattern of tubercles, or lack of tubercles, on funnel-mantle and nuchal fusion cartilages, and shape of the small, inner ocular photophore are useful features for specific identification.

GEOGRAPHICAL DISTRIBUTION.—Genus occurs circumglobally in tropical, subtropical, temperate, and subpolar regions and in the Antarctic.

REMARKS.—Ongoing studies (N. Voss) indicate that genus is composed of six to seven closely related species. Contiguous geographic distributions of congeners are typical of genus.

Galiteuthis armata Joubin, 1898

SPECIES CHARACTERS.—*Young:* Funnel-mantle fusion cartilages each with a 1–3-pointed tubercle (>25 mm ML); gladial tail long in juveniles; inner ocular photophore stout, bar-shape.

GEOGRAPHICAL DISTRIBUTION.—Atlantic in North Temperate, North Subtropical, and Tropical regions to ~10°S; East and West Mediterranean.

VERTICAL DISTRIBUTION.—Young < ~30 mm ML have been taken with closing gear from subsurface waters to 1000 m, but are concentrated in upper 200 m; juveniles > ~35 mm ML are usually found in depths >600 m; large subadults have been captured between 500 to >2500 m, but appear to be concentrated below ~1300 m.

REFERENCES.—Clarke and Lu (1975), N. Voss (unpublished data).

Galiteuthis glacialis (Chun, 1906)

SPECIES CHARACTERS.—*Young* (Figure 227): Nuchal fusion cartilage with a 2–3-pointed tubercle on each anterolateral angle (first seen as single-pointed tubercles at ~7–9 mm ML);

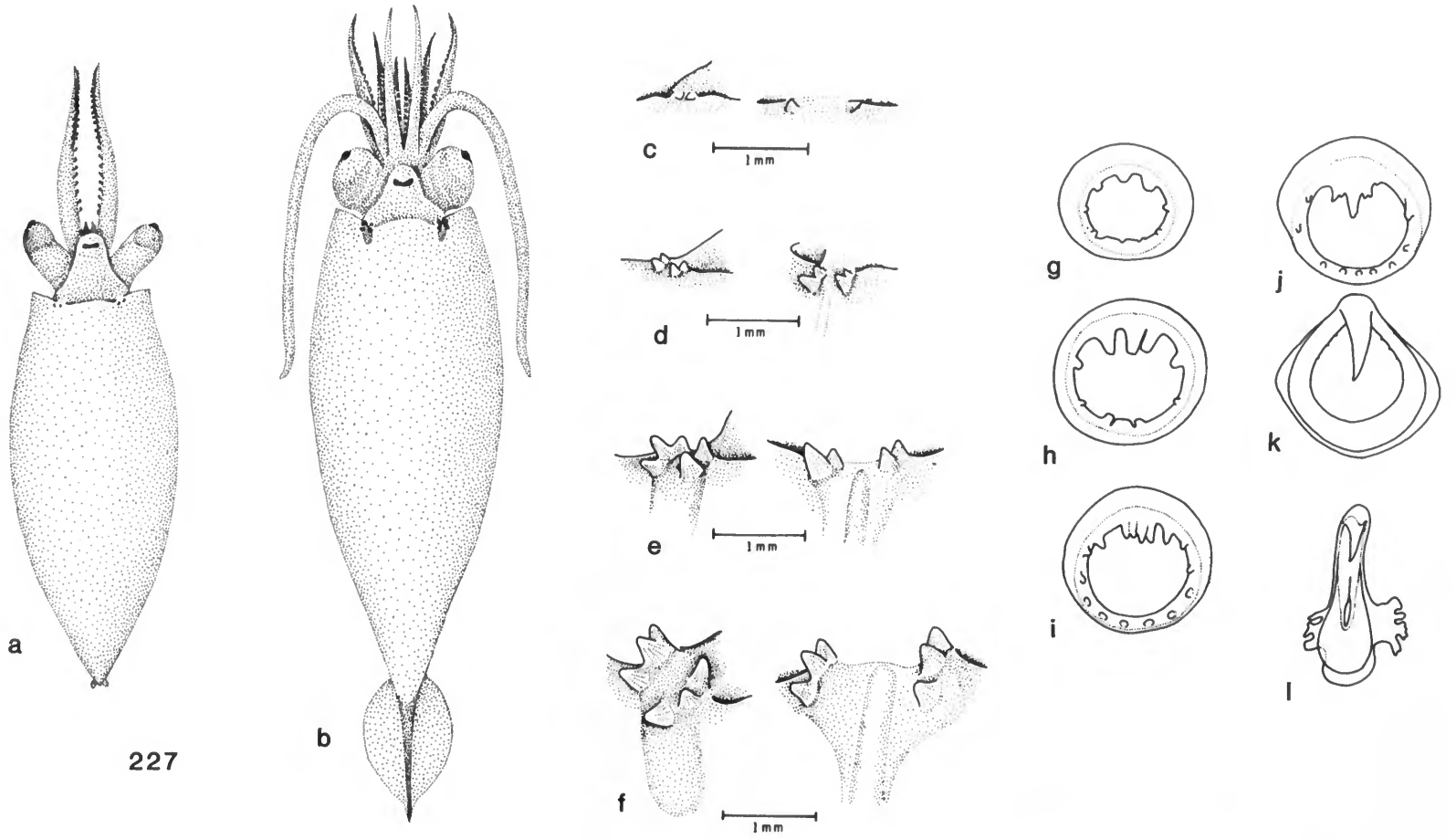

FIGURE 227.—*Galiteuthis glacialis*, Antarctic Ocean: *a*, ventral view, 11 mm ML; *b*, ventral view, 54 mm ML; *c–f*, tubercles on right funnel-mantle fusion cartilage and on nuchal cartilage: *c*, 7 mm ML; *d*, 16 mm ML; *e*, 24 mm ML; *f*, 55 mm ML; *g–l*, rings from largest tentacular club sucker: *g*, 29 mm ML; *h*, 38 mm ML; *i*, 55 mm ML; *j*, 58 mm ML; *k*, 73 mm ML; *l*, 297 mm ML (*a,b*, from N. Voss, 1980; *c–l*, from McSweeny, 1978).

funnel-mantle fusion cartilages each with two 2–3-pointed tubercles (first seen as 2 single-pointed tubercles at ~7–9 mm ML); gladial tail short; inner ocular photophore long, narrow.

GEOGRAPHICAL DISTRIBUTION.—Circumglobal in the Antarctic with some scattering north of the Antarctic Convergence.

VERTICAL DISTRIBUTION.—"Larvae" and juveniles are distributed between ~75 to >2000 m, with greatest concentration between ~300 to 1000 m. With growth, juveniles tend to concentrate at progressively greater depths within this range. Maturation occurs in deep water to >2500 m. Considerable diel vertical movement does occur.

REFERENCES.—McSweeny (1971, 1978), Rodhouse and Clarke (1986), N. Voss (unpublished data).

Galiteuthis phyllura Berry, 1911

SPECIES CHARACTERS.—*Young:* Funnel-mantle fusion cartilages each with a 2–4-pointed tubercle (seen at 16 mm ML); gladial tail short in juveniles; inner ocular photophore stout, bar-shape sometimes slightly curved.

GEOGRAPHICAL DISTRIBUTION.—Pacific Subarctic, and California Current to ~25°N.

VERTICAL DISTRIBUTION.—"Larvae" <10 mm ML concentrated in upper 100 m; with growth, "larvae" seek greater depths to ~500–600 m. After eyes become sessile, juveniles usually found below 800 m. Subadults have been captured between 440 and 1200 m.

REFERENCES.—Young (1972b), Nesis (1973b), Roper and Young (1975), N. Voss (unpublished data).

Galiteuthis pacifica (Robson, 1948)

SPECIES CHARACTERS.—*Young:* Funnel-mantle fusion cartilages without tubercles; gladial tail short; inner ocular photophore short, stout, nearly round (seen in juveniles > ~60 mm ML).

GEOGRAPHICAL DISTRIBUTION.—Pacific in equatorial and tropical waters; scattered north in Central Pacific to ~28°N, and in California Current to ~34°N; Peru-Chile Current north of ~30°S.

VERTICAL DISTRIBUTION.—"Larvae" < ~20 mm ML have been taken from subsurface to ~800 m; larger "larvae" to ~45 mm ML, when eyes become sessile, are concentrated between ~600 to 800 m; with growth juveniles seek progressively deeper water. Subadults have been taken between ~700 to 2000 m. There is no evidence of diel vertical migration.

REFERENCES.—Nesis (1973b), Young (1978), N. Voss (unpublished data).

Mesonychoteuthis Robson, 1925

REMARKS.—Single species, primarily restricted to Antarctic waters.

Mesonychoteuthis hamiltoni Robson, 1925

SPECIES CHARACTERS.—*Young* (Figure 228): Mantle stout, spindle-shape; mucous outer layer sometimes present; funnel-mantle fusion cartilages each with a 4–6-pointed tubercle (seen in larvae of 15 mm ML); nuchal cartilage with single, small tubercle at mid-anterior margin (seen in larvae of 15 mm ML); head with short, stout arm-crown stalk (< ~40–45 mm ML); eyes oval without ventral rostrum, on short, stout stalks (< ~40–45 mm ML); arms with hooks first seen forming on mid portions at ~45 mm ML; fins small, round, with projecting intervening short, broad gladial spine at ~20–25 mm ML. In juveniles, gladial spine does not project beyond round, combined outline of fins.

GEOGRAPHICAL DISTRIBUTION.—Circumglobal in Antarctic, with scattering in the Subantarctic.

VERTICAL DISTRIBUTION.—Poorly known. "Larvae" <30 mm ML have been taken in upper 500 m (shallowest capture, 20 m); larger "larvae" and juveniles are usually found between ~500 to >2000 m.

REMARKS.—Major food item for sperm whales in Southern Ocean.

REFERENCES.—McSweeny (1970), Klumov and Yukhov (1975), N. Voss (1980, unpublished data), Rodhouse and Clarke (1985).

Teuthowenia Chun, 1910

GENERIC CHARACTERS.—*Young:* Mantle stout, saccular (< ~11 mm ML), becomes increasingly conical with growth; mantle with numerous small to relatively few large, oval (when expanded; mere points when contracted), reddish brown chromatophores densely to widely spaced (seen as early as 4–5 mm ML); head with short, stout arm-crown stalk; eyes oval, with short ventral rostrum, on short, stout stalks; tentacles of medium length, usually stout, with 4 rows of suckers extending nearly entire length of stalks.

Note: Only genus in which carpal suckers occur in 4 rows on major portion of tentacular stalk. Chromatophore pattern on mantle, and tubercle configuration on funnel-mantle fusion cartilages are useful features for separating species.

GEOGRAPHICAL DISTRIBUTION.—Genus occurs in subarctic, north-temperate, and eastern tropical waters of Atlantic, and circumglobally in Southern Subtropical Convergence.

REMARKS.—Composed of three species. "Larval" stage is prolonged, persists to mantle lengths of ~53–100 mm ML. Distributional patterns of the species are disjunct (allopatric), but some areas of overlap may occur in the eastern Atlantic.

Teuthowenia megalops (Prosch, 1847)

SPECIES CHARACTERS.—*Young* (Figure 229*a–d*): Mantle with large (if expanded), widely spaced, oval chromatophores;

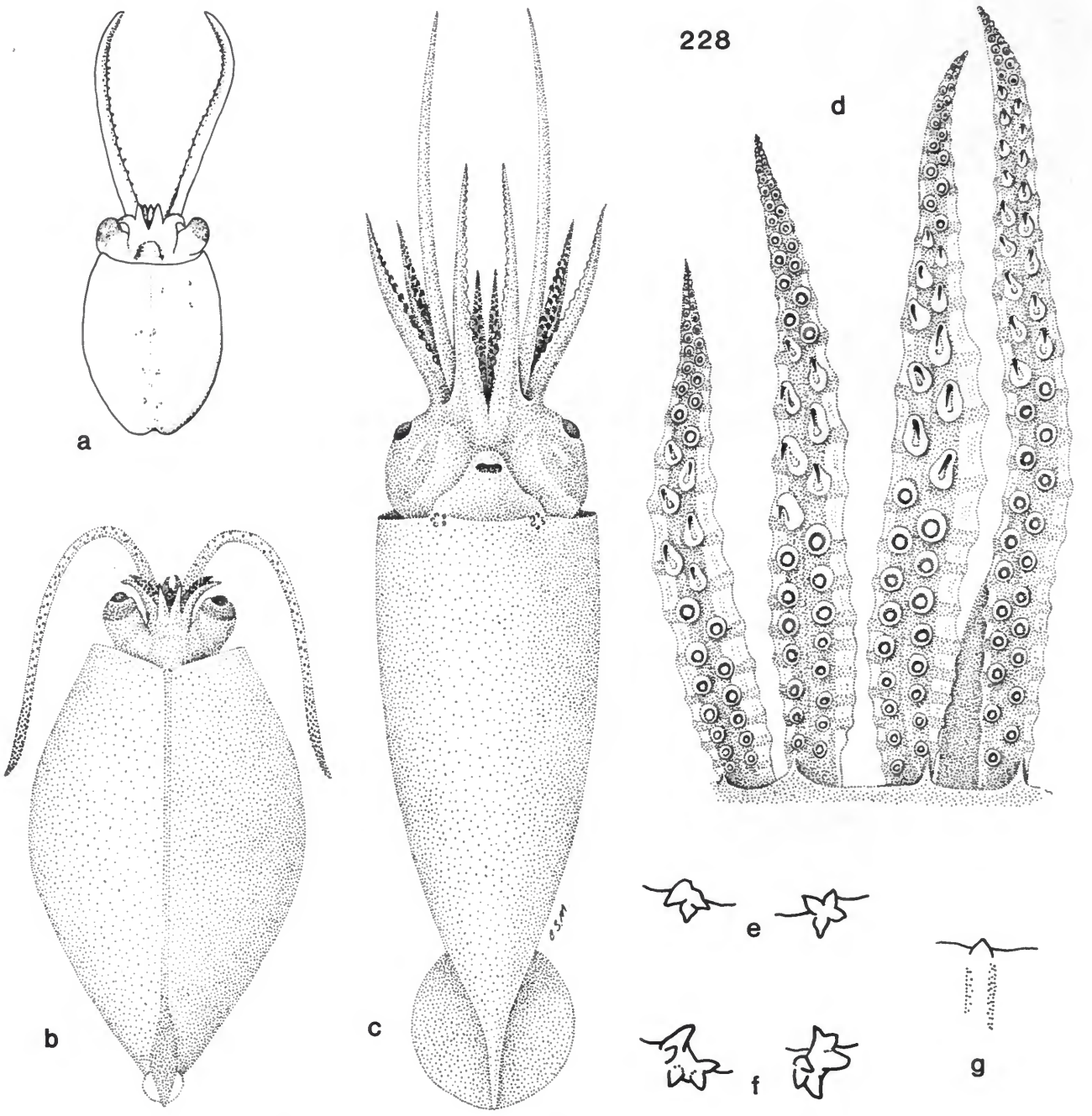

FIGURE 228.—*Mesonychoteuthis hamiltoni*, Antarctic Ocean: *a*, ventral view, 6 mm ML (from Rodhouse and Clarke, 1985); *b*, dorsal view, 23 mm ML; *c*, ventral view, 86 mm ML; *d*, left arms I-IV of same (*b–d*, from N. Voss, 1980); *e*, *f*, tubercles on right and left funnel-mantle fusion cartilages; *e*, 23 mm ML; *f*, 86 mm ML; *g*, tubercle on nuchal cartilage, 23 mm ML (*e–g*, redrawn from McSweeny, 1970).

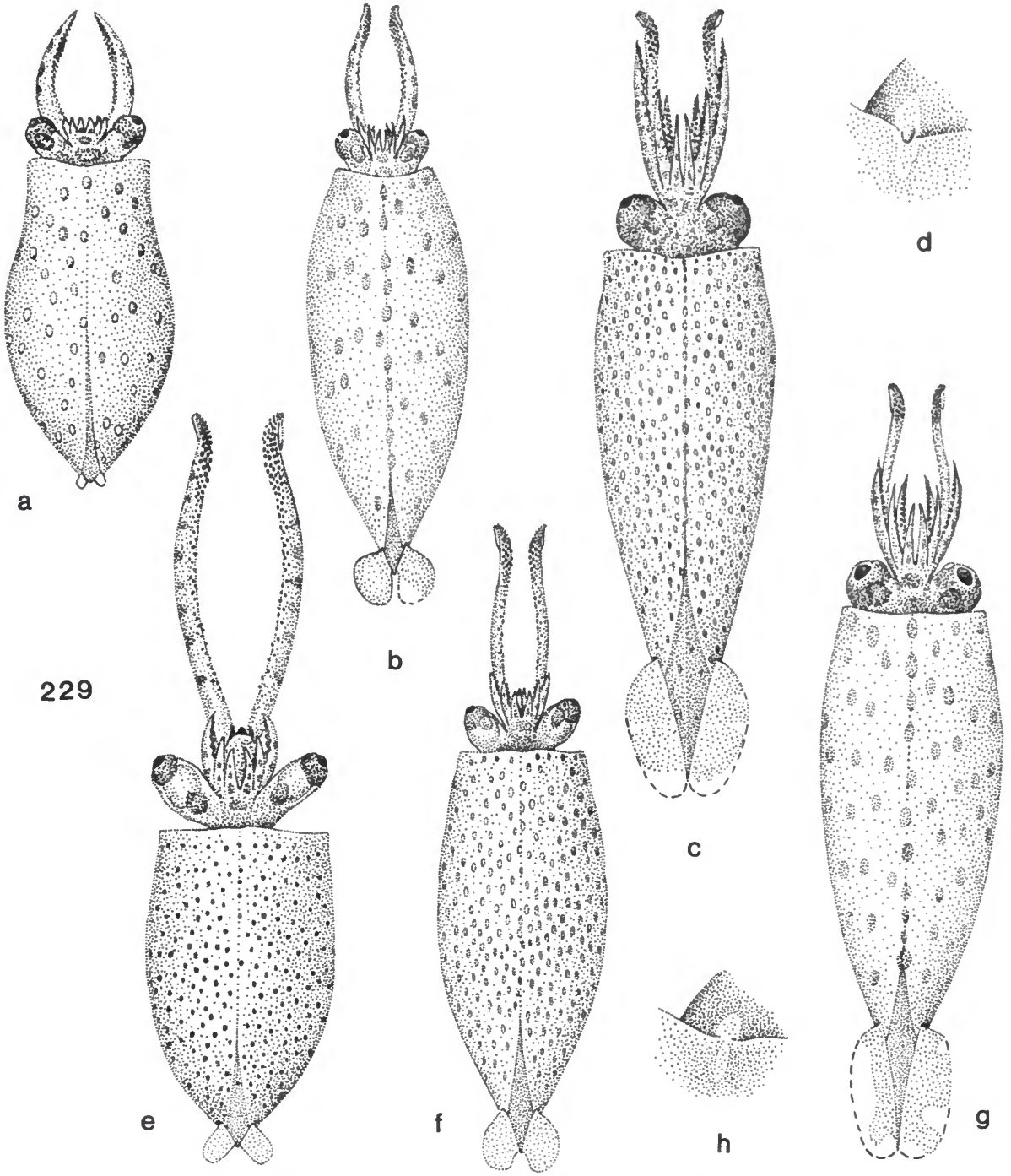

FIGURE 229.—*a–d, Teuthowenia megalops,* North Atlantic Slope water: *a,* dorsal view, 11 mm ML; *b,* dorsal view, 29 mm ML; *c,* dorsal view, 60 mm ML; *d,* right funnel-mantle fusion cartilage of same. *e–h, Teuthowenia maculata,* eastern Tropical Atlantic: *e,* dorsal view, 11 mm ML; *f,* dorsal view, 27 mm ML; *g,* dorsal view, 56 mm ML; *h,* right funnel-mantle fusion cartilage of same. (From N. Voss, 1985.)

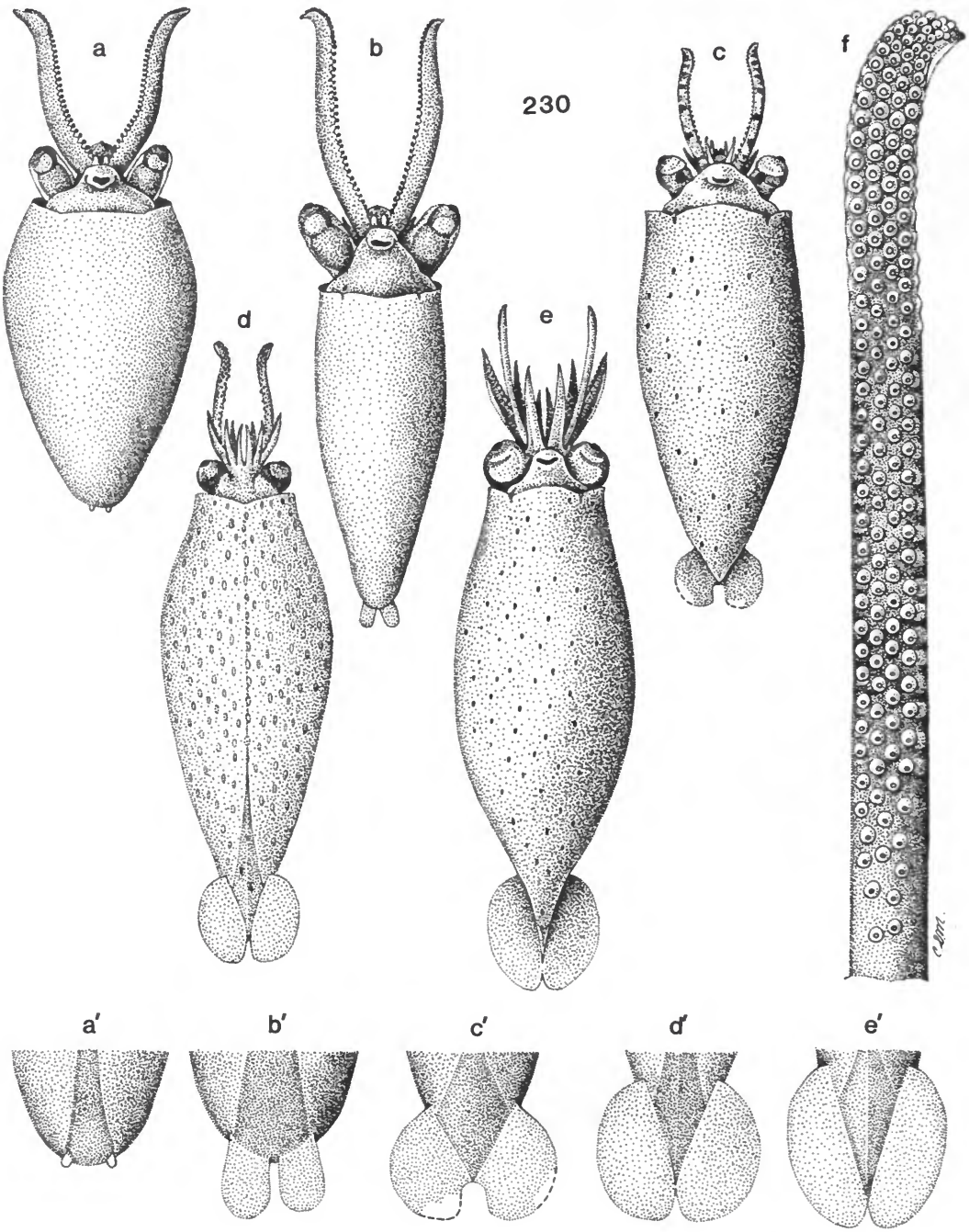

FIGURE 230.—*Teuthowenia pellucida*, vicinity of Southern Subtropical Convergence: *a–e*, developmental series of young (*a–c,e*, ventral views; *d*, dorsal view; *a′–e′*, posterior ends of mantle, dorsal views, showing development of fins and posterior end of gladius): *a,a′*, 7 mm ML; *b,b′*, 10 mm ML; *c,c′*, 27 mm ML; *d,d′*, 57 mm ML; *e,e′*, 85 mm GL. *f*, tentacle, 10 mm ML. (Chromatophores bleached in *a,b;* on mantle, shown contracted in *c,e;* expanded in *d.*) (From N. Voss, 1980.)

funnel-mantle fusion cartilages with single-point tubercle first seen in "larvae" at ~30–60 mm ML.

GEOGRAPHICAL DISTRIBUTION.—Atlantic, in Subarctic, and in high productivity areas of North Temperate Region.

VERTICAL DISTRIBUTION.—"Larvae" <10 mm ML have been taken from subsurface waters to ~1000 m; "larvae" of ~10–60 mm ML are concentrated in upper 200–300 m; with growth, "larvae" extend depth range to ~500 m. Following metamorphosis at ~75–95 mm ML, juveniles extend range to ~1000 m. There is evidence of diel vertical migration for juveniles and subadults. Maturation and spawning appear to occur in deep waters >1000 m.

REFERENCES.—Lu and Clarke (1975b; reported as *Taonius megalops*), Dilly and Nixon (1976; reported as *Taonius megalops*), N. Voss (1985).

Teuthowenia maculata (Leach, 1817)

SPECIES CHARACTERS.—*Young* (Figure 229*e–h*): Mantle with small, oval chromatophores densely spaced; funnel-mantle fusion cartilages with single-point tubercle usually lacking in "larvae," but seen in early juveniles at ~65–70 mm ML.

GEOGRAPHICAL DISTRIBUTION.—Eastern tropical Atlantic, including Mauritanean Upwelling.

VERTICAL DISTRIBUTION.—"Larvae" of ~6–20 mm ML appear to be concentrated in upper 100 m; late "larvae" > ~40 mm ML are found between ~300–600 m. Following metamorphosis at ~55–60 mm ML, juveniles increase their range to greater depths. There is evidence of some diel vertical movement.

REFERENCES.—Lu and Clarke (1975b; reported as *Taonius megalops*), N. Voss (1985).

Teuthowenia pellucida Chun, 1910

SPECIES CHARACTERS.—*Young* (Figures 230, 231): Mantle with medium-size, oval chromatophores moderately spaced (confined to posterior end of mantle at ~3 mm ML); funnel-mantle fusion cartilages with multipartite tubercle at > ~25–30 mm ML (single-point tubercle usually seen at ~10–20 mm ML).

Note: Size at which eyes become sessile varies widely from ~53–95 mm ML over broad geographic range of species.

GEOGRAPHICAL DISTRIBUTION.—Circumglobal in Southern Subtropical Convergence and fringing waters.

VERTICAL DISTRIBUTION.—"Larvae" < ~10 mm ML are distributed from the surface to ~600 m; young to ~70 mm ML may occur day and night in upper 200 m. Juveniles and early subadults are taken between ~700–800 m in the day and in upper 300 meters at night. Maturation occurs in depths of ~1500 to possibly >2400 m.

REFERENCE.—N. Voss (1985).

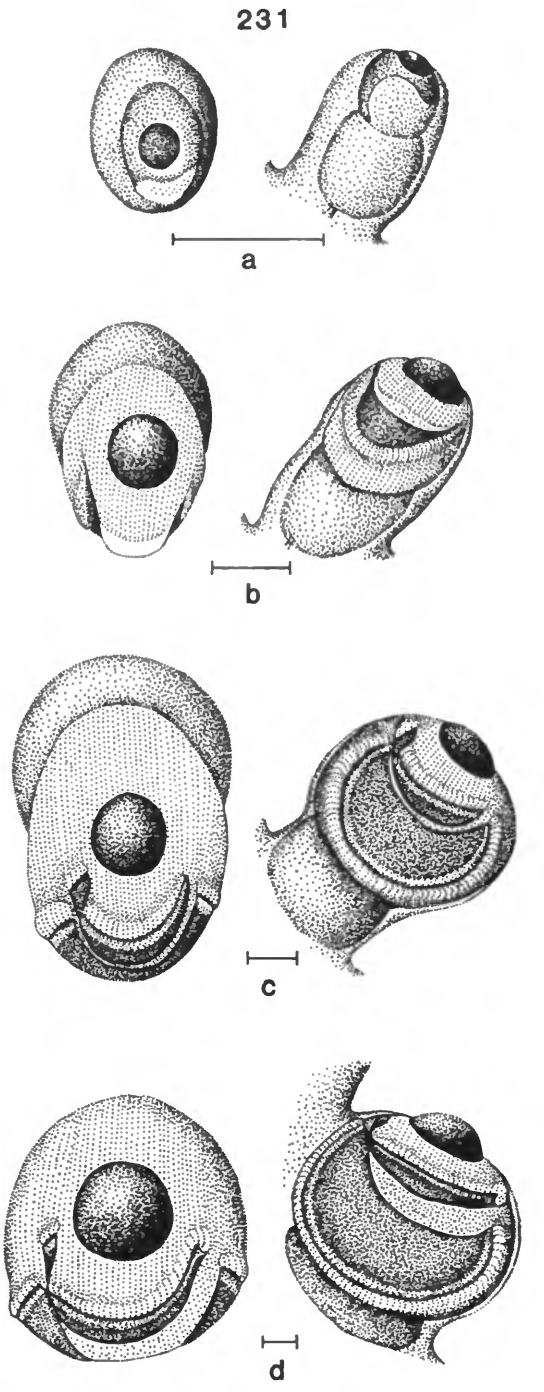

FIGURE 231.—*Teuthowenia pellucida*, vicinity of Southern Subtropical Convergence: *a–d*, ontogenetic series showing changes in shape of eye and development of ocular photophores, anterolateral and ventral views of left eye: *a*, 7 mm ML; *b*, 27 mm ML; *c*, 67 mm ML; *d*, 85 mm GL. Scale bar = 1 mm. (From N. Voss, 1985.)

Egea Joubin, 1933

REMARKS.—A single, cosmopolitan species currently is recognized; ongoing studies (N. Voss) indicate that genus may be composed of two species.

Egea inermis Joubin, 1933 (group)*

SPECIES CHARACTERS.—*Young* (Figure 232): Mantle elongate, spindle-shape; funnel-mantle fusion cartilages elongate, roughly triangular; fins small, terminal, paddle-shape, inserted on elongate, diamond-shape lanceola (~7–16 mm ML); fins rounded, extending onto lateral margins of mantle at > ~22 mm ML; head with short, stout, arm-crown stalk; eyes oval, with short ventral rostrum, on short to medium length stalks; tentacles long, narrow, with 2 rows of carpal suckers changing to 4 rows about 1 club length proximal to forming club.

GEOGRAPHICAL DISTRIBUTION.—Circumglobal in tropical and equatorial waters, extending into Gulf of Mexico and northwestern Atlantic in the Gulf Stream system, and into northwestern Pacific in the Kuroshio Current.

VERTICAL DISTRIBUTION.—"Larvae" of 7–~35 mm ML concentrated day and night in upper 200 meters; following metamorphosis (at ~35–40 mm ML), juveniles expand their range to at least 800 m. Night captures of juveniles and large subadults from subsurface to ~300 m indicate that at least part of population undergoes diel vertical movement. Maturation occurs in deep water to possibly 2000 m.

REFERENCES.—N. Voss (1974, unpublished data), Lu and Roper (1979), Lea (1984).

Megalocranchia Pfeffer, 1884

GENERIC CHARACTERS.—*Young* (Figure 233): Mantle moderately stout, spindle-shape with mucous outer layer often present; funnel-mantle fusion cartilages elongate, roughly triangular; fins small, inserted on moderately narrow, diamond-shape lanceola, with growth, become rounded and extend onto lateral margins of mantle; head with moderately long, arm-crown stalk; eyes oval, with short ventral rostrum, on long stalks; tentacles long, stout, with 2 rows of carpal suckers on basal half, 4 rows on distal half; compound photophore first seen forming on ventral surface of stout, spindle-shape digestive gland at ~25–30 mm ML.

GEOGRAPHICAL DISTRIBUTION.—Genus occurs circumglobally in subtropical, tropical, and equatorial waters.

VERTICAL DISTRIBUTION.—"Larvae" are concentrated between the surface and ~200 m day and night. Following metamorphosis at ~40–50 mm ML, juveniles are concentrated in the upper 200 m at night, and between about 600–800 m during the day. Subadults have been taken in deep water to >2000 m during the day and between ~700 and 100 m at night. Mature and (?) spent females have been taken floating on the surface at night in the Atlantic and Indian oceans indicating that spawning occurs in shallow water.

REMARKS.—Ongoing studies (N. Voss) indicate the genus may be composed of about six species. In recent literature some of the material from the Atlantic referred to *Corynomma speculator* Chun, *Megalocranchia abyssicola* (Goodrich), *Phasmatopsis cymoctypus* de Rochebrune, and *P. oceanica* (G. Voss), and material from the Pacific referred to *Corynomma abyssicola* (Goodrich), *Megalocranchia fisheri* Berry, and *Phasmatopsis fisheri* (Berry), belong to this genus. At present, only subadults and adults can be confidently identified to species. Congeners in all oceans may co-occur over considerable extents of ranges.

REFERENCES.—Roper and Young (1975), Young (1978), Lea (1984), N. Voss (unpublished data).

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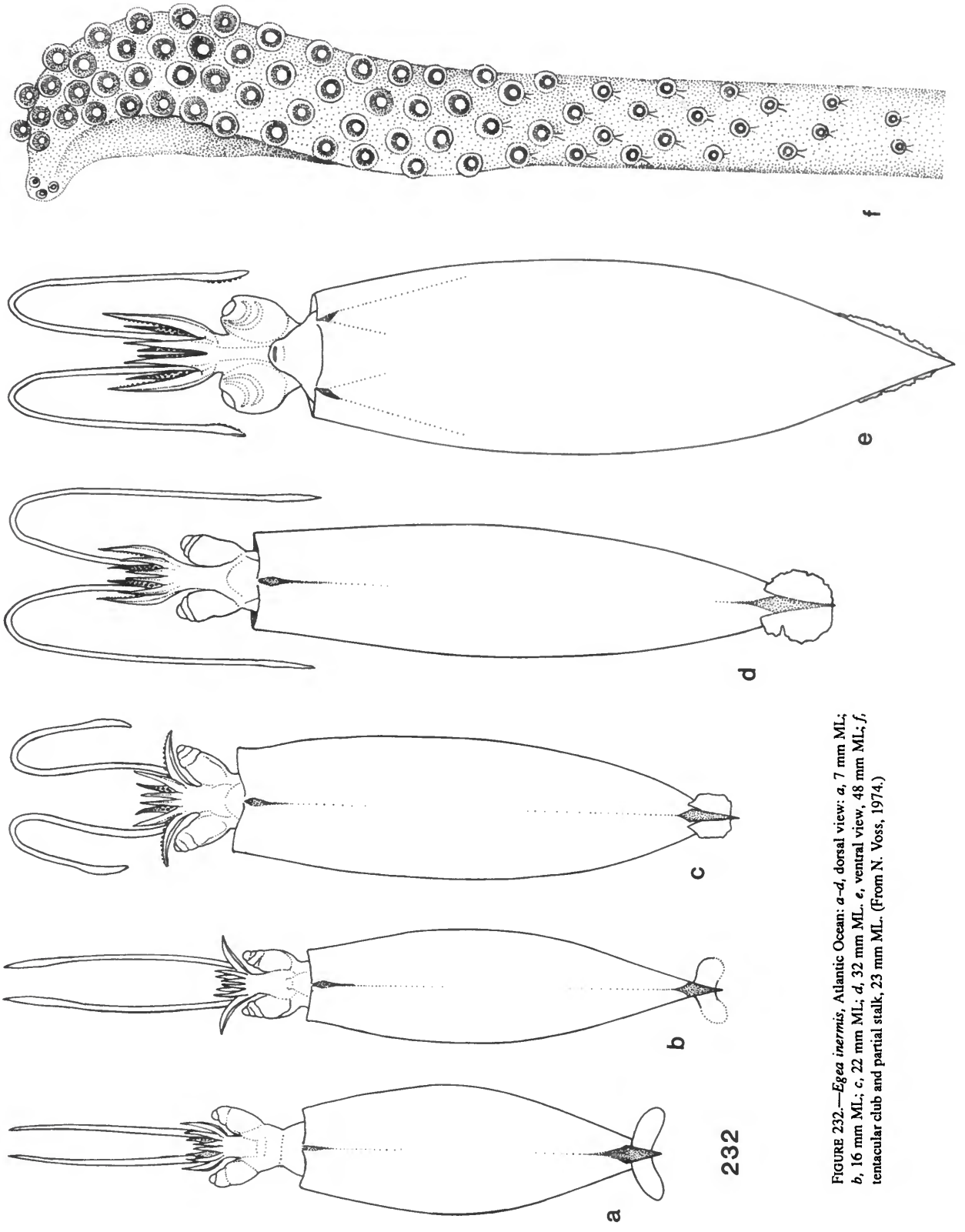

FIGURE 232.—*Egea inermis*, Atlantic Ocean: *a–d*, dorsal view: *a*, 7 mm ML; *b*, 16 mm ML; *c*, 22 mm ML; *d*, 32 mm ML. *e*, ventral view, 48 mm ML; *f*, tentacular club and partial stalk, 23 mm ML. (From N. Voss, 1974.)

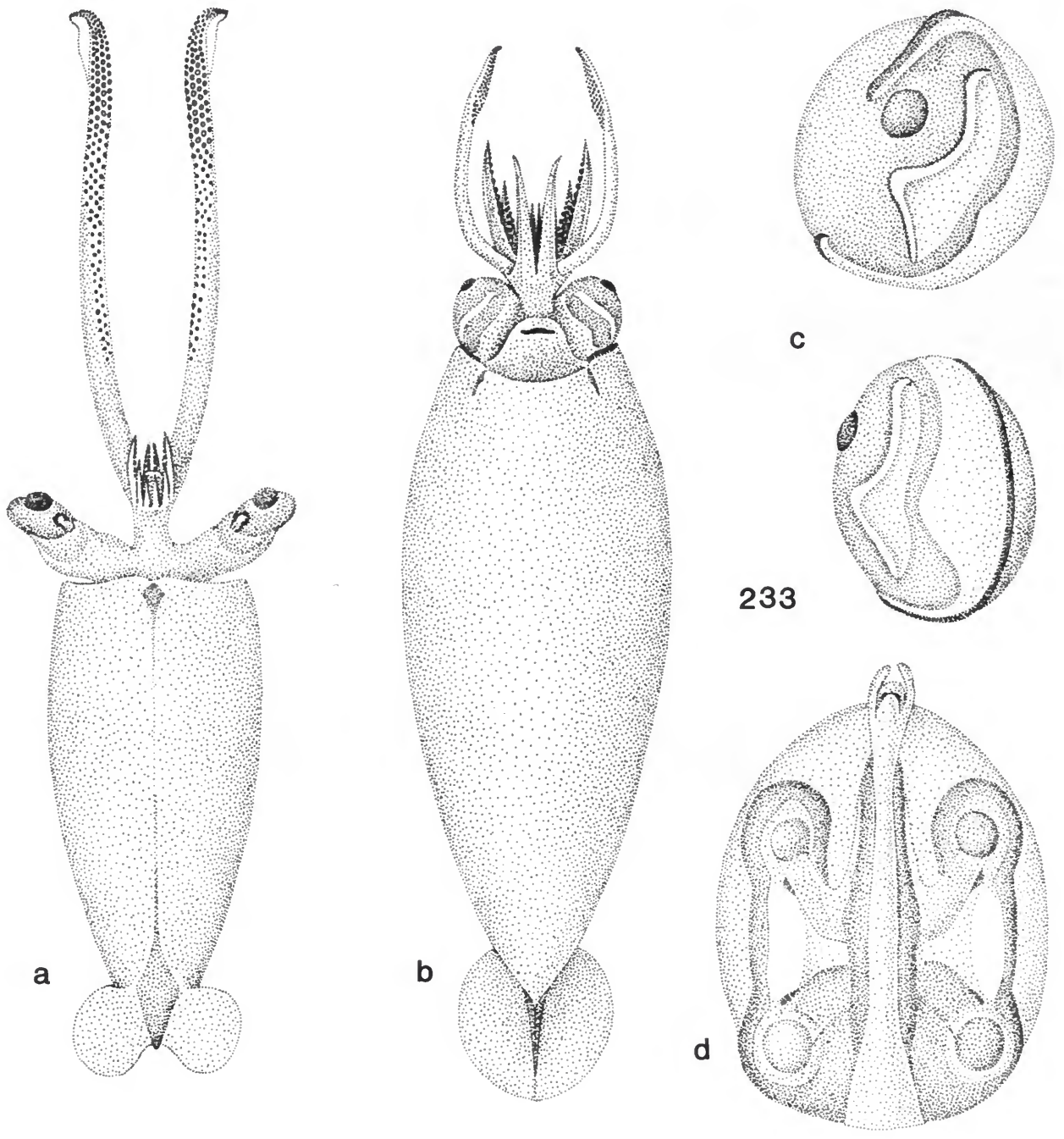

FIGURE 233.—*Megalocranchia* sp., North Atlantic Ocean: *a*, dorsal view, 17 mm ML; *b*, ventral view, 54 mm ML; *c*, right eye, lateral and ventrolateral views showing photophores, 82 mm ML; *d*, compound photophore on ventral surface of digestive gland, 82 mm ML. (From N. Voss, 1980.)

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Order VAMPYROMORPHA Pickford, 1939

(by F.G. Hochberg and M. Nixon*)

ORDINAL CHARACTERS.—Ten circumoral appendages; arms II represented by pair of long, slender velar filaments, without suckers, retractable into pockets between bases of arms I and III; other arms all identical; tentacles absent (i.e., ventro-lateral arm not differentiated into tentacles); radula homodont, unicuspid; web uniformly deep; cirri present, paired series, on oral surface of arms; suckers uniserial, stalked, without horny rings; body gelatinous; single pair, paddle-like fins present [except in young between 9-23 mm ML when 2 pairs present]; hectocotylus absent; oviducts paired; light organs present at base of each fin, medial to each eye, and scattered over mantle, head, and aboral surface of arms, several types; funnel with valve, sunken into tissue; mantle opening wide; mantle locking-apparatus absent; gladius large, nonmineralized; eyes large (diameter 40% ML), hemispherical; gills with up to 27 lamellae per outer demibranch; skin with black and dark red pigment, most chromatophores nonfunctional (i.e., without muscles).

Family VAMPYROTEUTHIDAE Thiele, 1915

FAMILY CHARACTERS.—*Adults:* With characters of the order. Monotypic.

Vampyroteuthis Chun, 1903

GENERIC CHARACTERS.—*Adults:* With characters of the family. Monotypic.

Vampyroteuthis infernalis Chun, 1903

SPECIES CHARACTERS.—*Adults* (Figure 234*a*): With characters of the genus.

Eggs (Figure 234*b*): Ripe ovarian eggs spherical, stalkless, 3.3 mm in diameter. Average diameter spawned eggs 3.8 mm (Pickford, 1949b, 1950).

Young (Figure 234*c-h*): Hatchling stage unknown. Youngest larva known, 5.5 mm ML. Arms of smallest specimens with cirri only, suckers lacking; suckers uniserial and stalked when they develop; single pair of lateral larval fins in larvae <9.0 mm ML (Pickford's stage I larvae); anterior pair of fin buds develop, rapidly overtake posterior "larval" fins in length in "larvae" >9.0 mm ML; by 25-30 mm ML the posterior "larval" fins resorbed; fin light organs present at 6.4 mm ML (Pickford, 1949a, 1950).

GEOGRAPHICAL DISTRIBUTION.—Cosmopolitan in tropical to temperate waters.

VERTICAL DISTRIBUTION.—Lower mesopelagic to bathypelagic. Off California, center of vertical distribution 500-1200 m. Young <20 mm ML generally occupy water deeper than 900 m. Adults and subadults occur primarily at depths <900 m, undergo ontogenetic ascent about the time the larval fins are resorbed (Roper and Young, 1975).

REMARKS.—Eggs, described by Pickford (1949b) from plankton collections could have been from ruptured adult females. Larval stages that are damaged during collection may be confused with bolitaenids, vitreledonellids, amphitretids, or cirrates. The best features to use in separating *Vampyroteuthis* young are the fins, photophores, velar filaments, gladius, black-pigmented skin, exceedingly large conspicuous beaks, stalked suckers, lack of suckers near mouth, cirri, and large hemispherical eyes. The digestive gland is ovoid, compact, and relatively small compared to the bolitaenids. The body length to arm length ratio is about 1:1. A deep web connects all the arms. In side view, larvae have large circular eyes. In dorsal view, the optic stalks are broad and attach directly to the brain without the well-defined lobe and stalk arrangement seen in squids. In dorsal view, the line from the left eye through the brain to the right eye is straight. The funnel is large and extends anteriorly well past the eye to the base of the arms.

REFERENCES.—Clarke and Lu (1974, 1975), Joubin (1937), Lu and Clarke (1975), Pickford (1946, 1949a, 1949b, 1950, 1952), Roper and Young (1975).

* Substantial reviews were provided by R.B. Toll and G.L. Voss.

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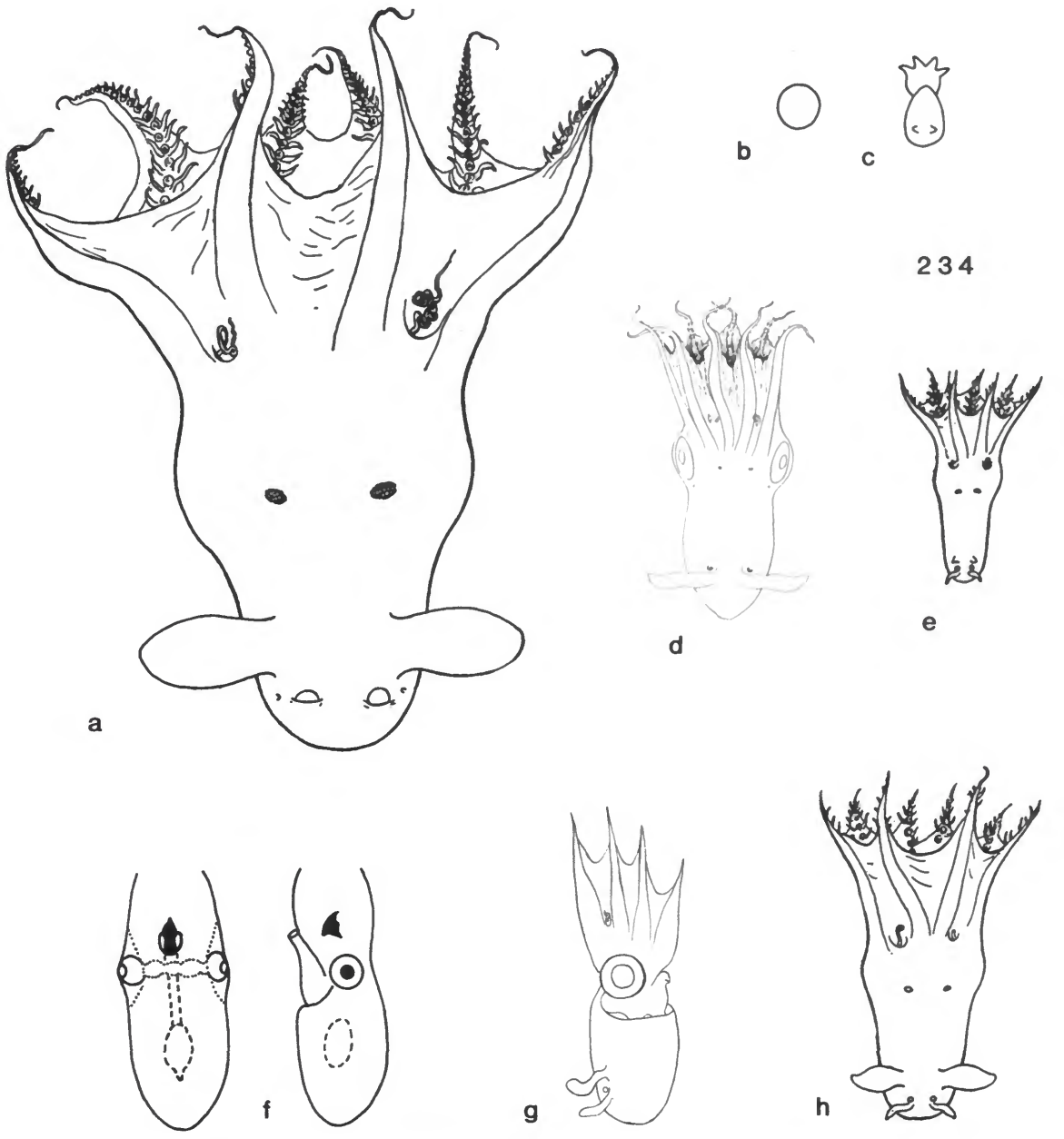


FIGURE 234.—Vampyroteuthidae, *Vampyroteuthis infernalis*, North Atlantic Ocean: *a*, dorsal view, adult male, 50 mm ML; *b*, spherical pelagic egg, 3.8 mm diameter; *c*, dorsal view, post hatchling with 1 pair larval fins, 5.5 mm ML; *d*, dorsal view, stage 1 larva with 1 pair larval fins, 7 mm ML; *e*, dorsal view, early stage 2 larva with second pair of fins emerging, 10 mm ML; *f*, dorsal and lateral views, diagnostic sketch of stage 2 larva to show relative sizes of beak, digestive gland, and eye, 12 mm ML; *g*, lateral view, stage 3 larva with larval and adult fins equal length, 18 mm ML; *h*, dorsal view, stage 4 larva with well-developed adult fins, just prior to resorption of larval fins, 25 mm ML (*a–c*, *e*,*h*, from Pickford, 1950; *d*,*g*, from Joubin, 1937; *f*, original).

Order OCTOPODA Leach, 1818

(by F.G. Hochberg, M. Nixon, and R.B. Toll*)

INTRODUCTION.—For the purposes of this contribution the finned octopod families in the suborder Cirrata are discussed first. In the suborder Incirrata, all the families that are pelagic, both as adults and larvae, are treated next. The family Octopodidae is treated last, as all adults are predominately benthic, but hatchlings and larvae of some species are pelagic. Table 4 summarizes the major characters separating the families of the orders Vampyromorpha and Octopoda. Table 5 summarizes size and number of eggs for the holopelagic Octopoda exclusive of Octopodidae. Table 6 summarizes size and number of eggs in the family Octopodidae. A worksheet (see Appendix 1) was formulated to aid in characterizing larval octopods. Figure 235 expresses general terminology used in this chapter or defines features used to identify or describe larval octopods. Additional figures relating to terminology are found at the beginning of the Octopodidae section. All figures are by Hochberg unless indicated otherwise.

ORDINAL CHARACTERS.—Eight circumoral arms; tentacles absent (i.e., ventro-lateral arms not differentiated into tentacles); velar filaments absent; fins, when present, paddle-like, subterminal, and widely separated; shell vestige, when present, well developed and single *or* reduced and paired; arm cirri present *or* absent; suckers uniserial *or* biserial, stalked *or* sessile, without horny rings; lens of eye covered with primary and secondary transparent lids (cornea); branchial canal generally present on gills between down-folded filaments; digestive duct appendages incorporated into digestive gland; radula present, reduced, vestigial, *or* absent, dentition homodont, heterodont, or ctenodont; buccal membrane absent; olfactory organ a ciliated pit; chromatophores present and functional (with muscles) *or* absent.

Suborder CIRRATA Grimpe, 1916

SUBORDINAL CHARACTERS.—Paired lateral fins present, large, blade- or paddle-shape; paired arm cirri present, alternating with suckers; suckers uniserial, sessile, or stalked; web deep, delicate; body gelatinous and fragile *to* firm and muscular; mantle opening small; radula reduced and homodont *or* absent; chromatophores absent, skin pigmented, color other than black; shell vestige present as a relatively large fin support; right oviduct absent; ink sac absent; mantle locking-apparatus absent; hectocotylus absent; enlarged suckers present on arms of mature males.

REMARKS.—For revision of this poorly known group of deep-sea octopods see Voss (1988a, 1988b). Eight nominal genera and 30 nominal species currently are recognized and variously placed in the following three families: Cirroteuthidae Keferstein, 1866; Stauroteuthidae Grimpe, 1916; Opisthoteuthidae Verrill, 1896. Little general information is available on the reproductive biology and none on larval development of the cirrates.

Family CIRROTEUTHIDAE Keferstein, 1866

FAMILY CHARACTERS.—*Adults:* Body relatively elongate (i.e., not compressed), gelatinous, and fragile; eyes reduced *or* degenerate; skin lightly pigmented; web deep; secondary web present; cirri long, conspicuous; fins large, wide, longer than head width; shell vestige thick wing- or saddle-shape fin support; crop simple; gills "sepioid"; salivary glands present; a true radula absent; pallial adductor weakly developed.

REMARKS.—Two genera, *Cirroteuthis* and *Cirrothauma* are recognized.

Cirroteuthis Eschricht, 1836

GENERIC CHARACTERS.—*Adults:* Fin support compact, rectangular, wings slightly flared; mantle aperature narrow; funnel long; funnel organ inverted V; eyes with lenses; suckers little modified. Monotypic.

Cirroteuthis muelleri Eschricht, 1836

SPECIES CHARACTERS.—*Adults:* With characters of genus.

Eggs: Ovoid, large, 10–11 mm long; figured by Eschricht (1836).

Young (Figure 236*c*): Smallest postembryonic stage caught in plankton, 11 mm ML identified as *Cirroteuthis* sp. (Robson, 1924).

GEOGRAPHICAL DISTRIBUTION.—Arctic/boreal in North Pacific or North Atlantic.

VERTICAL DISTRIBUTION.—Benthopelagic; generally below 2000 m to at least 5000 m.

REFERENCES.—Eschricht (1836); Reinhardt and Prosch (1846); Robson (1924, 1932a); Voss (1988a, 1988b).

Cirrothauma Chun, 1911

GENERIC CHARACTERS.—*Adults* (Figure 236*a*): Fin support with widely flared wings; mantle aperture closed around long, slender funnel; funnel organ indistinct; eyes cup-like, without lenses; suckers strongly modified. Monotypic.

Cirrothauma murrayi Chun, 1911

SPECIES CHARACTERS.—*Adults* (Figure 236*a*): With characters of genus.

Eggs: Largest egg in oviduct 14.0 × 0.9 mm, ovoid, with tough brown outer coating and rudiments of stalk; small number of eggs in ovary and large size range suggests eggs

* Junior authors listed alphabetically. Substantial reviews were provided by S.v. Boletzky and G.L. Voss. Workshop participation and contributions by P.R. Boyle, J.W. Forsythe, R.T. Hanlon, M. Lang, and C. Sousa-Reis.

TABLE 4.—Summary of major family characters in the Orders Vampyromorpha and Octopoda (+, character present; √, character present but weakly developed; -, character absent; +/-, character present or absent; R, right; L, left; #, chromatophores present but lack muscles except near fins over photophores).

Family	*Nominal genera and (species)*	*Adult habit: P, pelagic; Bp, benthopelagic; B, benthic*	*Filaments*	*Funnel valve*	*Fins*	*Arm cirri*	*Shell vestige*	*Light organs*	*Suckers: S, stalked; s, sessile*	*Sucker rows*	*Radula type*	*Oviducts*	*Hectocotylized arm III in male*	*Hectocotylus in sac, detachable*	*Dwarf males*	*Mantle-funnel locking-apparatus*	*Body: G, gelatinous; M, firm/muscular*	*Mantle water pores*	*Secondary shell (ovarium)*	*Koelliker's bristles*	*Chromatophores*	*Pallial adductor*	*Ink sac*	*Crop*	*Posterior salivary gland*	*Cornea: O, open; C, closed*
Vampyroteuthidae	1(1)	P	+	+	+	+	+	+	S	1	homodont	2	-	-	-	-	G	-	-	-	#	-	-	+	+	O
Cirroteuthidae	2(2)	Bp/B	-	-	+	+	+	-	S	1	vestigial *or* absent	1	-	-	-	-	G	-	-	-	-	+	-	√	+	O
Stauroteuthidae	5(>15)	Bp/B	-	-	+	+	+	-	S	1	absent	1	-	-	-	-	G	-	-	-	-	-	-	√	-	O
Opisthoteuthidae	1(>8)	Bp/B	-	-	+	+	+	-	S	1	homodont *or* absent	1	-	-	-	-	M	-	-	-	-	-	-	-	-	O
Bolitaenidae	4(>4)	P	-	-	-	-	-	+	s	1	ctenodont	2	R/L	-	-	-	G	-	-	-	+	+	+	+	-	O
Amphitretidae	1(1)	P	-	-	-	-	-	-	s	1	ctenodont	2	R	-	-	-	G	-	-	-	+	+	+	+	+	O
Vitreledonellidae	1(1)	P	-	-	-	-	-	-	s	1	heterodont	2	L	-	-	-	G	-	-	-	+	+	+	+	-	O
Alloposidae	1(1)	P	-	-	-	-	-	-	s	1-2	heterodont	2	R	+	-	+	G	-	-	+	+	+	+	+	-	O
Tremoctopodidae	1(2)	P	-	-	-	-	√	-	s	2	heterodont	2	R	+	+	+	M/G	+	-	+	+	+	+	+	-	O
Ocythoidae	1(1)	P	-	-	-	-	-	-	s	2	heterodont	2	R	+	+	+	M	+	-	+	+	+	+	+	-	O
Argonautidae	1(6)	P	-	-	-	-	-	-	s	2	heterodont	2	L	+	+	+	M	-	+	+	+	+	+	+	-	O
Octopodidae	25(>200)	B	-	-	-	-	√	-	s	1/2	heterodont	2	R/L	-	-	-	M/G	*	-	+/-	+	+	+/-	+/-	+	C

* The genus *Cistopus* has arm pockets but they are not homologous to circumorbital water pores of *Tremoctopus* and *Ocythoe*.

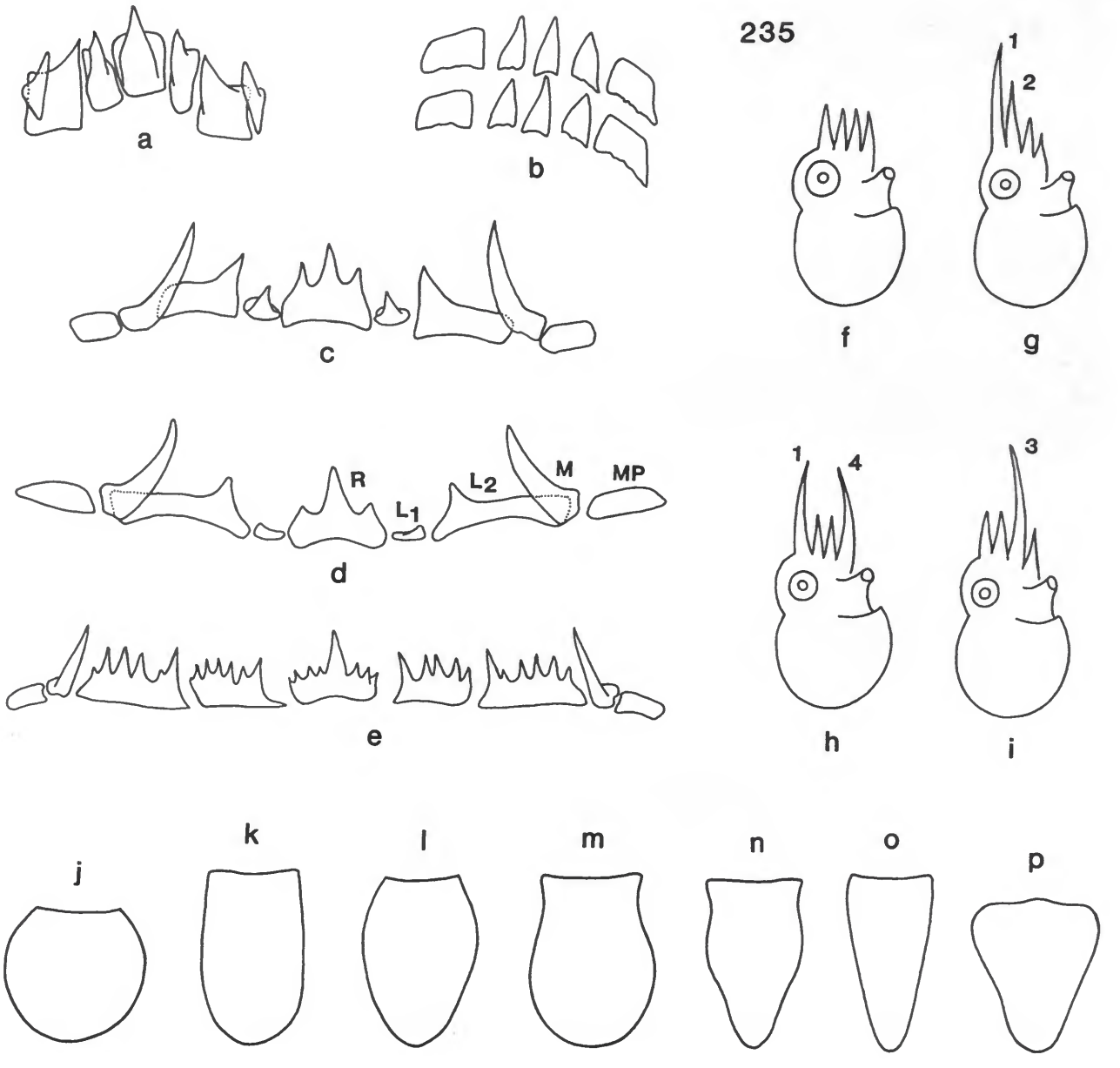


FIGURE 235.—Terminolgy for Order Octopoda, *a–e*, variations in radula dentition (abbreviations: R = rachidian; L1 and L2 = laterals; M = marginal; MP = marginal plate): *a*, homodont, *Vampyroteuthis* (from Pickford, 1949); *b*, homodont, *Grimpoteuthis* (after G. Voss, 1988a); *c*, heterodont, *Tremoctopus* (from Adam, 1937); *d*, heterodont, *Octopus* (from G. Voss, 1968); *e*, ctenodont, *Japetella* (from Adam, 1937). *f–i*, arm length patterns (original): *f*, subequal (*Octopus*); *g*, 1 > 2 > 3 > 4; *h*, 1 = 4 > 2 = 3; *i*, 3 > 1 = 2 > 4. *j–p*, variations in mantle shape (original): *j*, globose; *k*, cylindrical; *l*, ovoid; *m*, flask; *n*, amphora; *o*, conical; *p*, shield.

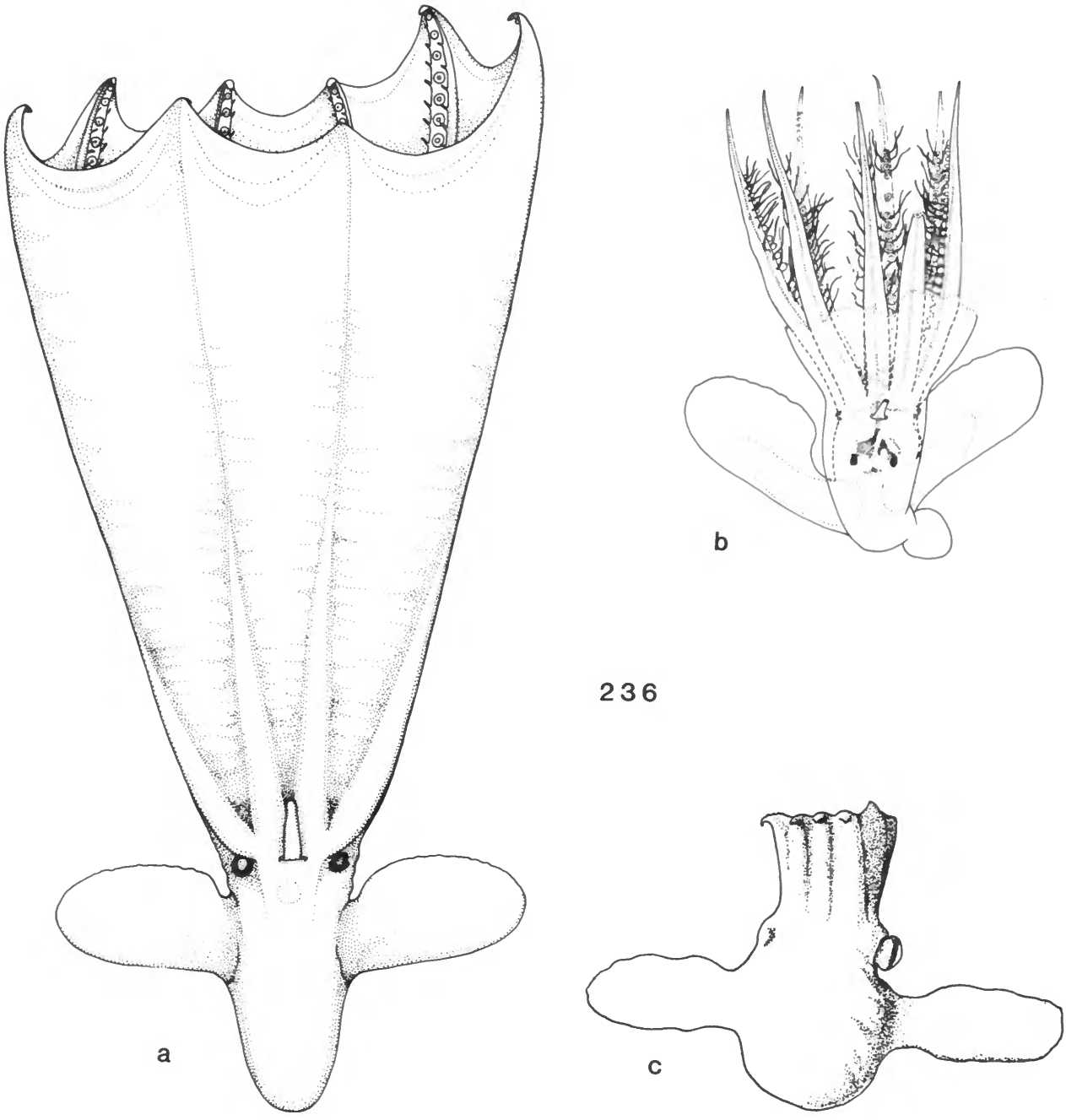


FIGURE 236.—Cirroteuthidae: *a,b, Cirrothauma murrayi,* ventral views, eastern North Atlantic (from Aldred et al., 1983): *a,* adult male, 155 mm ML; *b,* young, 20 mm ML. *c, Cirroteuthis* sp., dorsal view, young, 11 mm ML, eastern South Atlantic (off S. Africa) (from Robson, 1924).

TABLE 5.—Egg size and egg number in the pelagic Octopoda exclusive of the Cirrata and the Octopodidae (* = mature ovarian eggs).

Species	Egg capsule size range (mm)	Egg number	Reference
Alloposus mollis	1.5*	–	Thore (1949); Willassen (1986)
Amphitretus pelagicus	5*	–	Thore (1949)
Argonauta argo	0.6–0.8	11,200–48,000	Kubota and Miyashita (1975); Naef (1928)
Argonauta boettgeri	0.85–1.1	–	Nesis (1977)
Argonauta hians	0.7–0.8	–	Akimushkin (1965); Nesis (1972, 1977); Stephens (1965)
Bolitaena microcotyla	2.5–3.0	–	Robson (1931); Thore (1949)
Eledonella pygmaea	2.0	–	Thore (1949); Young (1972b)
Japetella diaphana	2.5–3.0	–	Thore (1949)
Ocythoe tuberculata	1.75–2.0*	100,000–104,000	Naef (1923, 1928); Roper and Sweeney (1976)
Tremoctopus violaceus	3.0–3.6	139,000	Hamabe (1973); Naef (1928); Sasaki (1929)
Vitreledonella richardi	3.8*	–	Thore (1949)

mature in small numbers, laid singly, egg laying continuous process once maturity attained; most likely laid on bottom (Aldred et al., 1983).

Young (Figure 236*b*): Juvenile specimen 10–15 mm ML, translucent, resembles miniature adult except fins enormously large and cirri disproportionately long compared to adults.

GEOGRAPHICAL DISTRIBUTION.—Cosmopolitan in all seas.

VERTICAL DISTRIBUTION.—Benthopelagic (or epibenthic); generally below 1500 m to at least 5000 m.

REFERENCES.—Aldred et al., (1983), Ebersbach (1915), Pearcy and Beal (1973), Roper and Brundage (1972), Roper and Young (1975), Voss (1988a, 1988b).

Family STAUROTEUTHIDAE Grimpe, 1916

FAMILY CHARACTERS.—*Adults:* Body gelatinous to semigelatinous, fragile, elongate to short, not compressed; secondary web present; fins small, longer than wide; shell vestige a V-shape fin support; gills "sepioid"; pallial adductor present; radula present *or* absent.

REMARKS.—Two genera, *Stauroteuthis* and possibly *Chunioteuthis*, are included in this family (Voss, 1988a, 1988b). Only the former is included here.

Stauroteuthis Verrill, 1879

GENERIC CHARACTERS.—*Adults:* With characters of family. Monotypic.

Stauroteuthis syrtensis Verrill, 1879

SPECIES CHARACTERS.—*Adults:* With characters of genus.

Eggs: Eggs, with embryos, measure 11 × 6 mm, attached to gorgonians (Verrill, 1885).

Young: Planktonic stages unknown.

GEOGRAPHICAL DISTRIBUTION.—Western North Atlantic.

VERTICAL DISTRIBUTION.—Benthopelagic; 450–2500 m.

REMARKS.—Unidentified eggs and embryos (Figure 237), most likely from cirroteuthids or stauroteuthids, have been described and figured by Boletzky (1978–1979, 1980, 1982, 1986). Egg capsules are characterized as being large (lengths 12–24 mm), with ribs, flutings, or longitudinal stripes. Compared with adults, the embryos have very large fins. All embryos so far examined have very large outer yolk sacs.

REFERENCES.—Boletzky (1978–1979, 1980, 1982, 1986), Robson (1924, 1932a), Verrill (1879, 1885), Voss (1988a, 1988b).

Family OPISTHOTEUTHIDAE Verrill, 1896

FAMILY CHARACTERS.—*Adults:* Body semigelatinous to firm, anteriorly-posteriorly compressed, disk-shape, or bell-shape; mantle aperture small; funnel short; funnel organ inverted V; cirri short; eyes large; web single, deep; secondary web absent; fins small, shorter than head width *or* large; fin support straight, V- or U-shape; radula present *or* absent; crop absent; posterior salivary glands reduced in size *or* absent; gills "half orange" type.

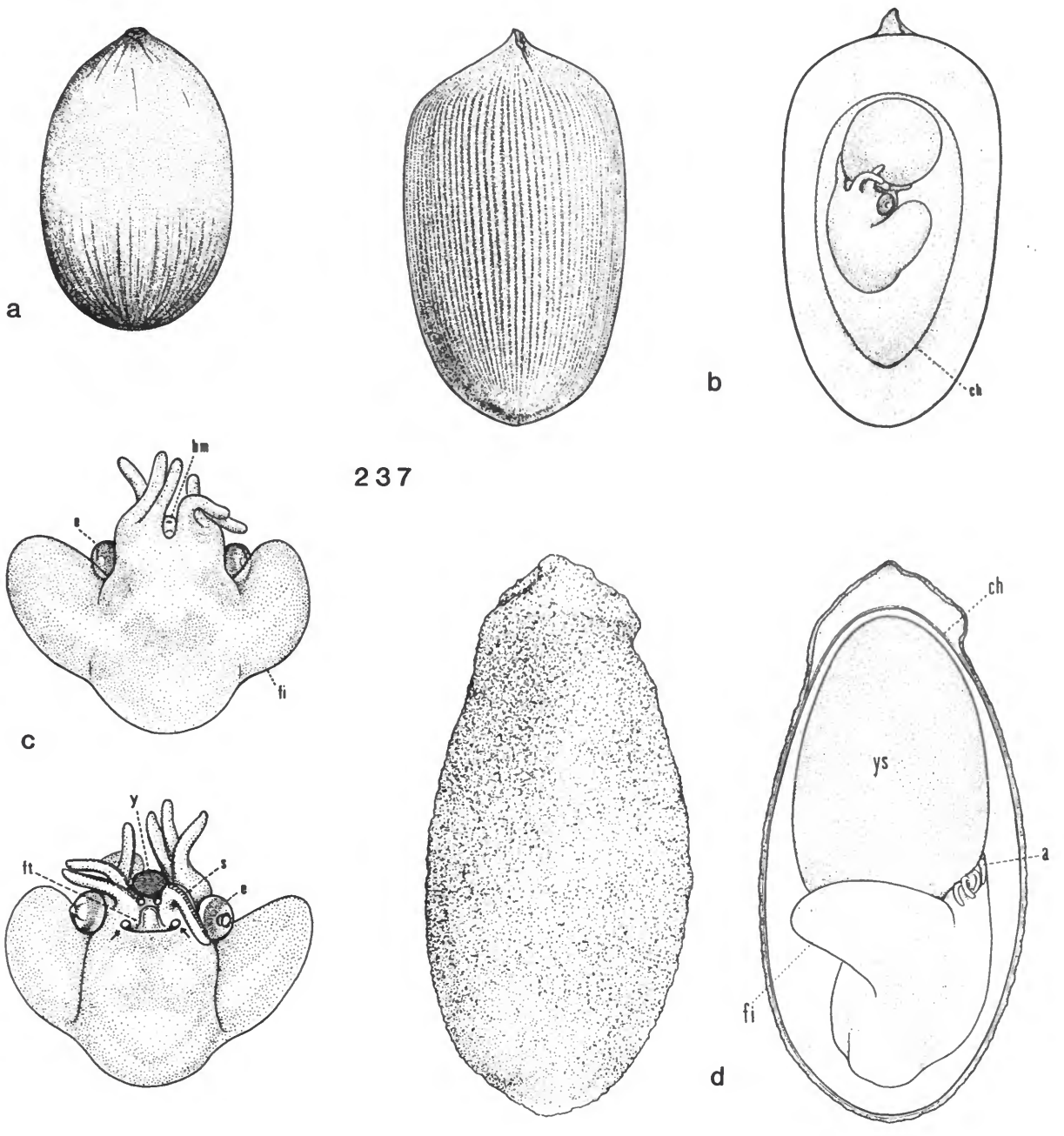


FIGURE 237.—Unidentified cirromorphs, Stauroteuthidae?: *a*, egg capsule, 12.5 mm CL, South Pacific; *b*, egg capsule (outer aspect) and with egg shell removed to expose chorion and embryo, 16 mm CL, Indian Ocean; *c*, dorsal and ventral views of embryo from *b*, 3 mm ML; *d*, egg capsule (outer aspect) and with egg shell removed to expose chorion and embryo, 24 mm CL, Indian Ocean (bm = buccal mass; ch = chorion; CL = capsule length; e = eye; f = fin; fl = funnel; s = sucker; y = yolk). (From Boletzky, 1982.)

REMARKS.—Two genera, *Opisthoteuthis* and *Grimpoteuthis*, and over 20 species currently recognized.

Opisthoteuthis Verrill, 1883

GENERIC CHARACTERS.—*Adults:* With characters of family.

Opisthoteuthis spp.

SPECIES CHARACTERS.—*Adults* (Figure 238*a*): Shell broadly open, U-shape to nearly straight rod; fins small, subterminal to superior; radula absent; optic nerves to eyes large, 2–5 in number; optic lobe large, flattened, kidney-shape; white body dark; mature males with enlarged suckers near base of arms and margins of web; body flattened, disk-shape.

Eggs (Figure 238*b*): *O. californiana:* maximum egg size in ovary, 9 × 5 mm (Berry, 1952); in oviduct, 11 × 6 mm (Pereyra, 1965); >75% of eggs may be ripe with many packed in oviduct ready for deposition (Pereyra, 1965). *O. vossi:* ripe ovarian eggs measure 9.9 mm (Sanchez and Guerra, 1989). *O. depressa:* ovarian eggs figured by Meyer (1906). Undescribed species from California: largest eggs in oviduct 7 × 4 mm (Hochberg, original observation).

Young (Figure 238*c*): In smallest specimens, arms with suckers only, cirri develop in later juvenile stage; juveniles compressed compared to adults.

GEOGRAPHICAL DISTRIBUTION.—Cosmopolitan, in tropical and temperate seas.

VERTICAL DISTRIBUTION.—Young probably planktonic; adults benthic, 100–2250 m, concentrated at 100–1000 m.

REMARKS.—Small planktonic juvenile (~15 mm ML) figured by Berry (1912).

REFERENCES.—Berry (1912, 1949, 1952, 1955), Meyer (1906), Pereyra (1965), Robson (1932a), Sanchez and Guerra (1989), Taki (1963), Voss (1988a, 1988b).

Grimpoteuthis Robson, 1932

GENERIC CHARACTERS.—*Adults:* With characters of family.

Grimpoteuthis spp.

SPECIES CHARACTERS.—*Adults* (Figure 239*a*): Fin support V- or U-shape; fins lateral to subterminal; optic lobe large, round; optic nerves to eyes branched, numerous; radula present in some species; body bell-shape.

Eggs: G. antarctica: ripe ovarian eggs ellipsoid, 16 × 12 mm (Kubodera and Okutani, 1986). *G.* (= *Stauroteuthis*) *albatrossi:* ovarian eggs 10 × 7 mm (Sasaki, 1929).

Young (Figure 239*b,c*): In smallest specimens, arms with suckers only, cirri develop in later juvenile stage; fins large compared to adults (Berry, 1917; Hoyle, 1886).

GEOGRAPHICAL DISTRIBUTION.—Atlantic, Pacific, and Antarctic Oceans.

VERTICAL DISTRIBUTION.—Young planktonic; adults benthic, 200–7000 m.

REMARKS.—Planktonic stages, tentatively identified as *Grimpoteuthis*, measure 12.5 and 15 mm ML.

REFERENCES. Berry (1917), Hoyle (1885, 1886, 1904), Joubin (1903), Kubodera and Okutani (1986), Robson (1932a), Sasaki (1920, 1929), Voss (1982, 1988a, 1988b).

Suborder INCIRRATA Grimpe, 1916

SUBORDINAL CHARACTERS.—Fins absent; arm cirri absent; suckers sessile, uniserial or biserial; body gelatinous *or* muscular; radula well developed *or* degenerate; skin with functional, mobile chromatophores; ink sac well developed, reduced, *or* absent; shell vestige reduced to pair of rod-like stylets *or* absent; mantle locking-apparatus present *or* absent; oviducts paired; in males hectocotylus present *or* absent, when present the entire arm modified or end organ restricted to tip of arm; luminescent tissue rarely present.

Family AMPHITRETIDAE Hoyle, 1886

FAMILY CHARACTERS.—*Adults:* Suckers uniserial; web deep, between all arms; body sac-like, gelatinous; mantle opening reduced to 2 small openings lateral to funnel (often difficult to find in preserved specimens); funnel fused to mantle; tip of right arm III hectocotylized, abruptly set off from rest of arm by conspicuous angular swelling; eyes tubular, directed dorsally; shell vestige absent; radula ctenodont; digestive gland large, ovoid, posterior to stomach; funnel organ W-shape; inner demibranch of gills reduced. Monotypic.

Amphitretus Hoyle, 1885

GENERIC CHARACTERS.—*Adults:* With characters of family. Monotypic.

Amphitretus pelagicus Hoyle, 1885

SPECIES CHARACTERS.—*Adults* (Figure 240*a,b*): With characters of genus.

Eggs: Mature eggs not known; mature ovarian eggs, measuring 5 × 2 mm, figured by Thore (1949).

Young (Figure 240*c*): Hatchling stage unknown. Young

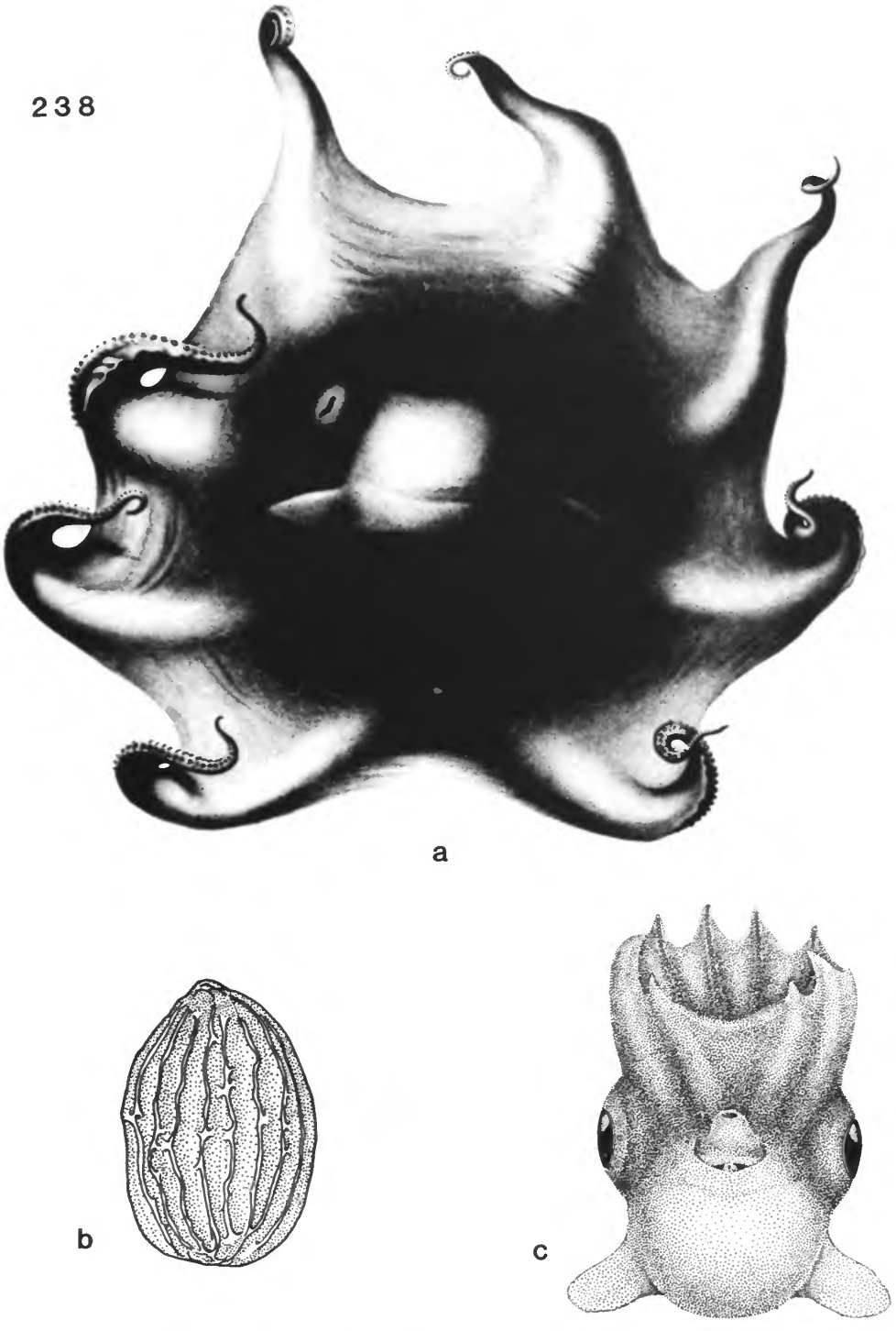


FIGURE 238.—Opisthoteuthidae: *a, Opisthoteuthis extensa,* posterior view, adult, Indian Ocean (from Chun, 1915). *b,c, Opisthoteuthis* sp. nov.: *b,* egg capsule, 7 mm CL (capsule length), off California; *c,* ventral view, young, 15 mm ML, eastern North Pacific (*b,* original; *c,* from Berry, 1912).

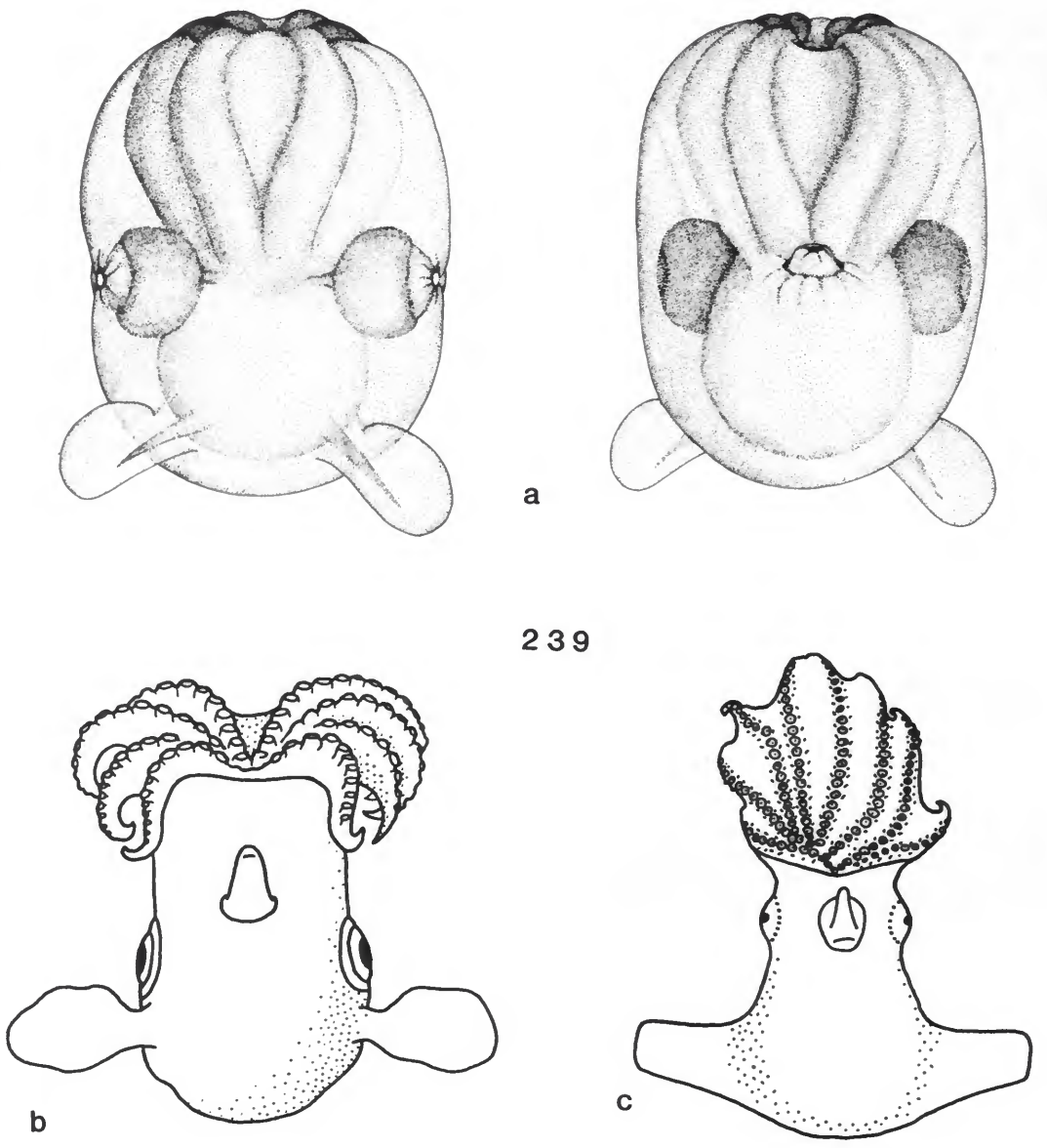


FIGURE 239.—Opisthoteuthidae: *a, Grimpoteuthis bruuni,* dorsal and ventral views, subadult male, 29 mm ML, eastern South Pacific (from G. Voss, 1982); *b,* unknown (possibly *G. meangensis*), ventral view, young, 15 mm ML, western South Pacific (redrawn from Hoyle, 1885); *c, G. mawsoni,* ventral view, young, 12.5 mm ML, Antarctic (from Berry, 1917).

specimen of 7 mm TL had same characteristics as adults (Thore, 1949); larva of 4 mm ML figured by Allan (1945).

GEOGRAPHICAL DISTRIBUTION.—Cosmopolitan.

VERTICAL DISTRIBUTION.—Mesopelagic to bathypelagic; from 150 m possibly to depths of 2000 m. Juveniles <30 mm TL found in surface waters in depths <150 m.

REMARKS.—*Idioctopus gracilipes* described by Taki (1962, see also Taki, 1963) and placed in the family Idioctopodidae maybe a synonym of *Amphitretus pelagicus.* The hectocotylus of *Idioctopus* has a slender, finely pointed tip and is set off from

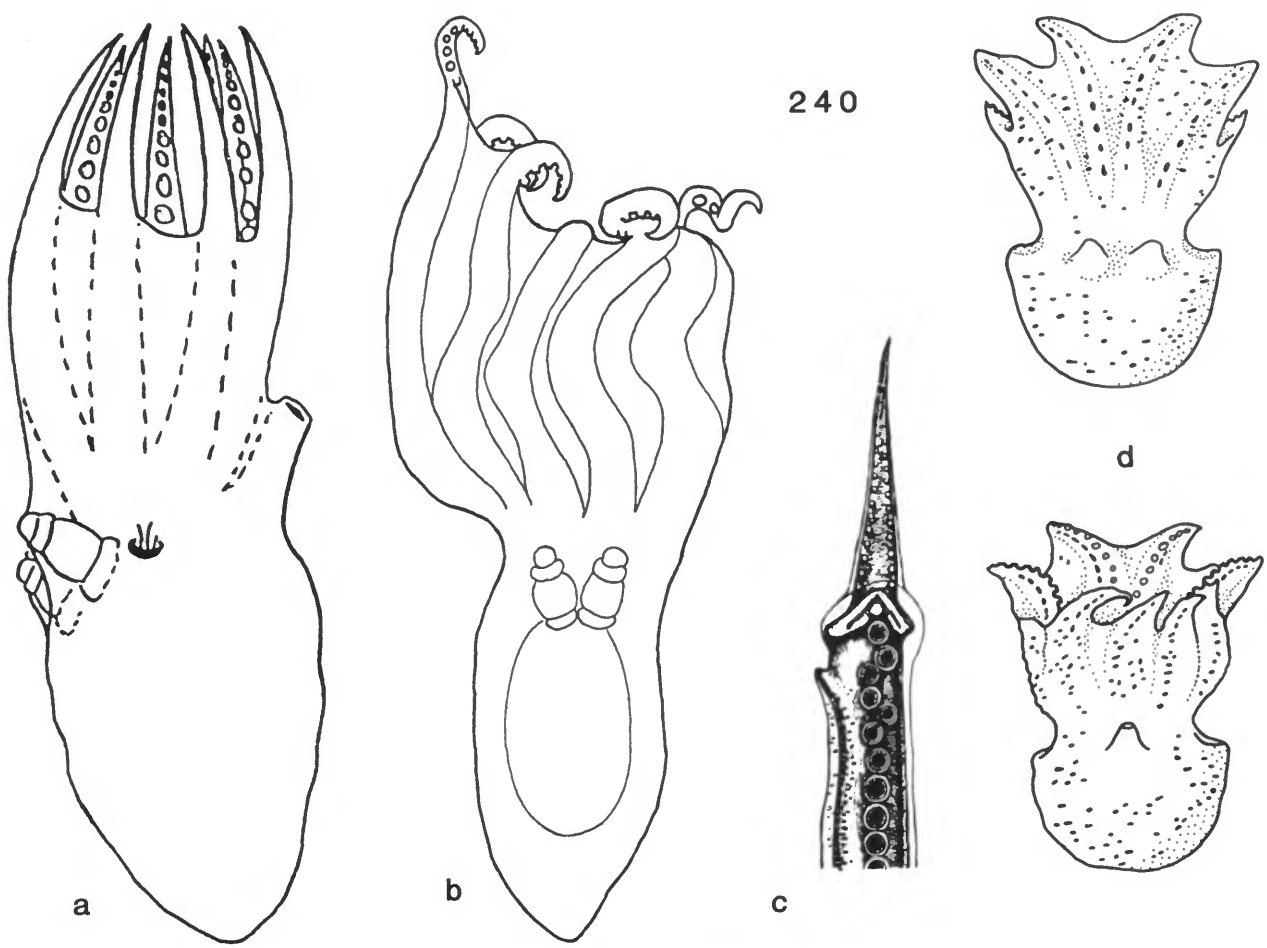


FIGURE 240.—Amphitretidae, *Amphitretus pelagicus: a*, lateral view, adult female, central Pacific (R.E. Young, original); *b*, dorsal view, adult male, eastern central Pacific (from Thore, 1949); *c*, details of hectocotylus, adult male, western Pacific (from Sasaki, 1917a); *d*, dorsal and ventral views, young, 4 mm ML, western South Pacific (from Allan, 1945).

the rest of the arm by a swelling similar to that observed in *Amphitretus*. However, until Taki's type specimen is available for comparison, the generic placement of *Idioctopus* cannot be finally resolved.

REFERENCES.—Allan (1945), Ijima and Ikeda (1902), Robson (1932a), Roper and Young (1975), Sasaki (1917a), Thore (1949).

Family BOLITAENIDAE Chun, 1911

FAMILY CHARACTERS.—*Adults* (Figures 241*a,b*, 242*a,b*): Suckers uniserial; web deep on all arms; mantle gelatinous, often with thick, jelly-like outer coating; mantle opening single, wide; radula ctenodont; digestive gland large, elongate-ovoid, anterior to stomach; eyes medium size, diameter <30% ML, elliptical, directed laterally; hectocotylization present as enlarged suckers on right or left arm III, not detachable; shell vestige absent; mantle locking-apparatus absent; inner demibranch of gills reduced; single mantle opening; funnel organ inverted V-shape; circumoral light organ present in mature females.

Eggs: Net collected eggs, attributed to *Eledonella* and *Japetella* figured by Thore (1949); larger eggs, 3.0 × 2.0 mm, with 3.0 mm stalk; smaller eggs, 2.5 × 1.0 mm with 1.0 mm stalk. (Additional material is needed to resolve the identity of these eggs.) Eggs of both *Japetella* and *Eledonella* are

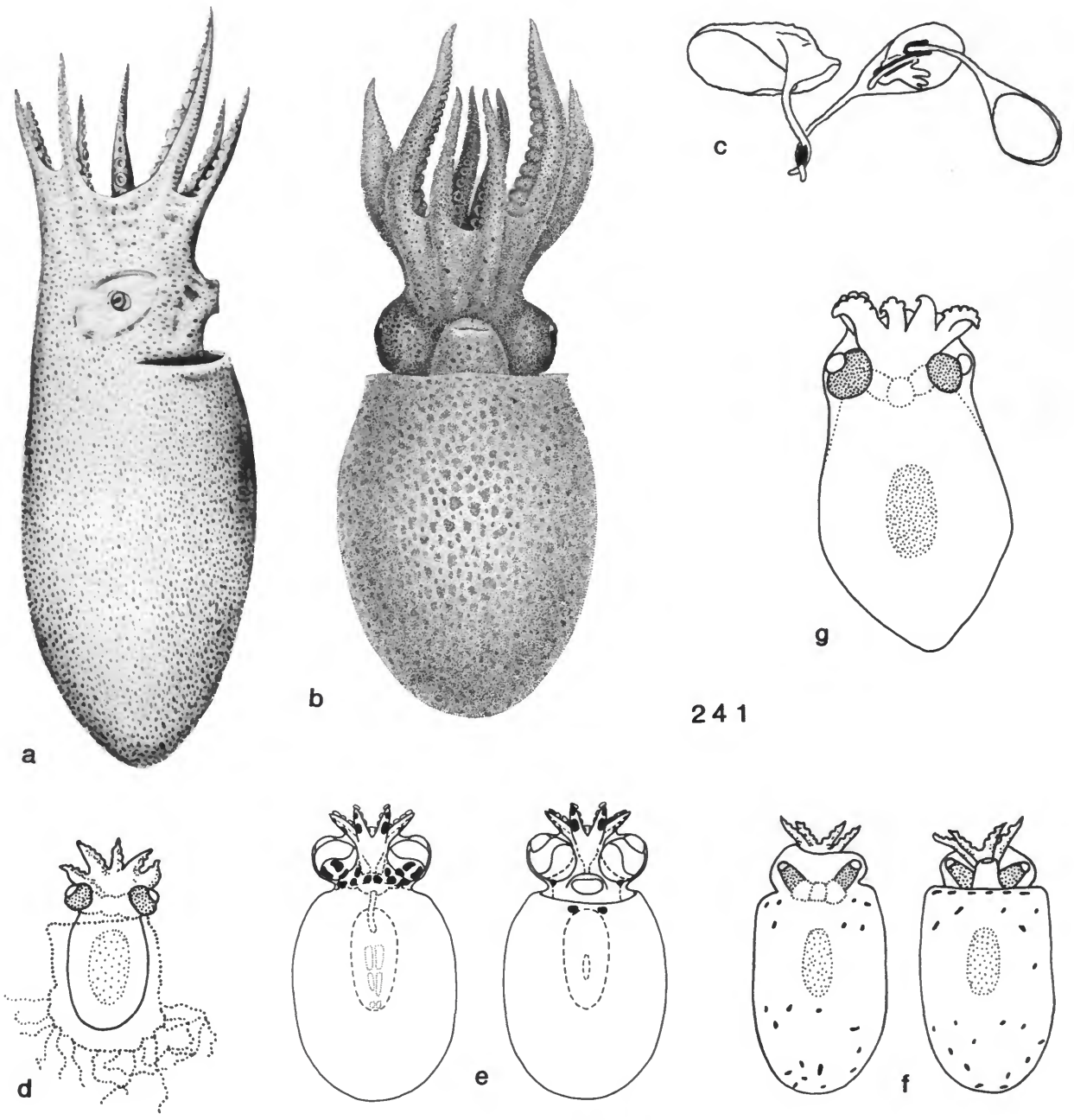


FIGURE 241.—Bolitaenidae, *Japetella diaphana: a*, lateral view, adult male, 78 mm ML, eastern North Pacific (from R.E. Young, 1972a); *b*, ventral view, adult female, 70 mm ML, eastern North Pacific (from Berry, 1912); *c*, egg capsule, 3 mm CL (capsule length), eastern Indian Ocean (from Thore, 1949); *d*, dorsal view, hatchlings with jelly-like coat, 3 mm ML, Indian Ocean, (redrawn from Thore, 1949); *e*, dorsal and lateral views, young, 3.8 mm ML, Hawaiian waters (R.E. Young, original); *f*, dorsal and ventral views, young, 7 mm ML, eastern North Pacific, (redrawn from Green, 1973); *g*, dorsal view, young, 12 mm ML, western North Pacific (redrawn from Thore, 1949).

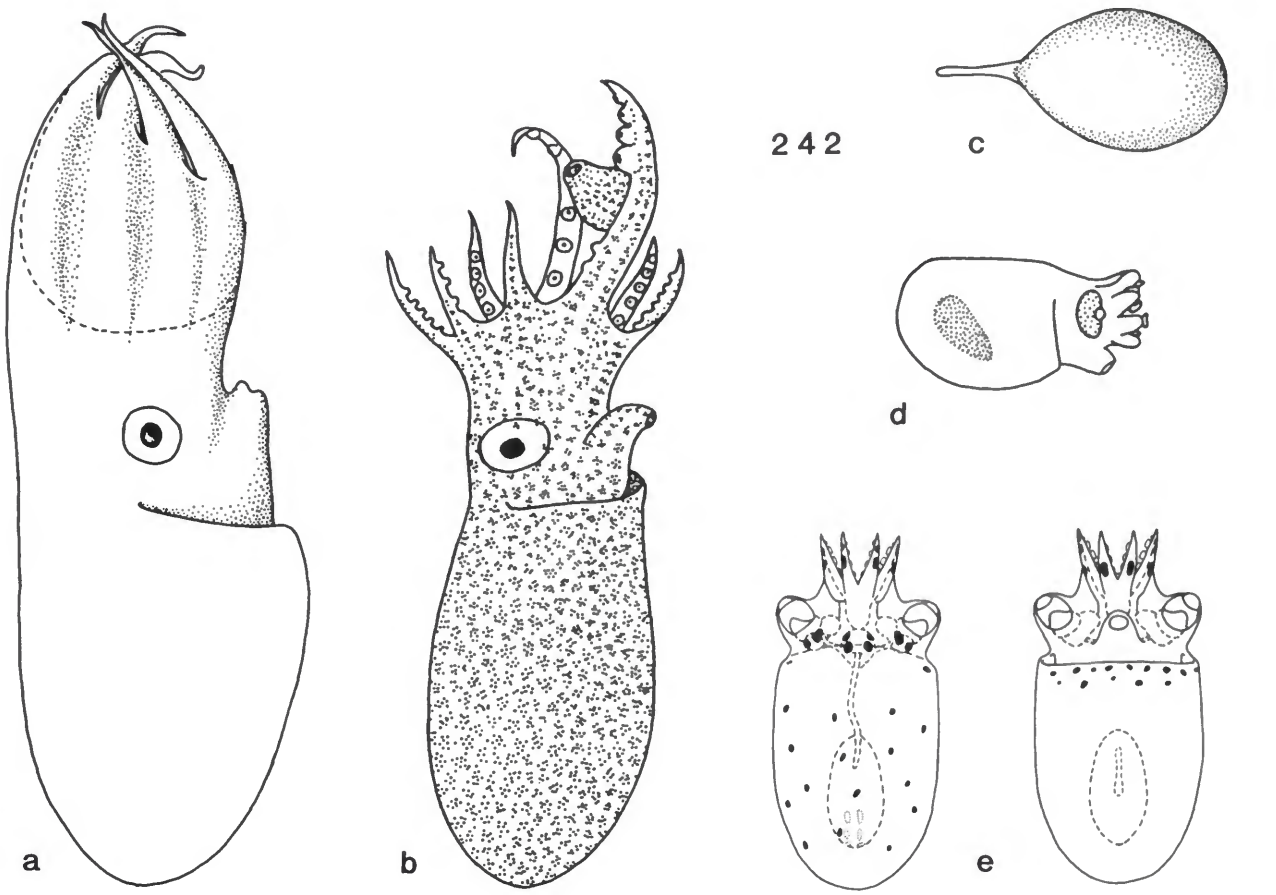


FIGURE 242.—Bolitaenidae, *Eledonella pygmaea: a,* lateral view, adult female brooding eggs, 35 mm ML, Hawaiian waters (from R.E. Young, 1972b; mistakenly refered to as *Bolitaena microtyla*); *b,* lateral view, adult male, eastern North Atlantic (redrawn from Chun, 1915); *c,* egg capsule, 2 mm CL (capsule length), Hawaiian waters (from R.E. Young, 1972b); *d,* lateral view, optical section, hatchling, 2 mm ML, Hawaiian waters (from R.E. Young, 1972b); *e,* dorsal and ventral views, young, 3.9 mm ML, Hawaiian waters (R.E. Young, original).

cemented together in large clusters and brooded within the brachial web of the female.

Young: Similar to adults, gelatinous, with elliptical eyes, single mantle opening and elongate-ovoid digestive gland.

REMARKS.—All members of this family are characterized by extremely soft and gelatinous bodies often damaged during capture or handling. Four genera have been described, *Bolitaena, Dorsopsis, Eledonella,* and *Japetella.* All are monotypic. *B. microtyla* Hoyle, 1886 is poorly known and is of questionable validity. Two other genera, represented by *E. pygmaea* and *J. diaphana,* are discussed below. A second species of *Japetella, J. heathi,* is known only from the eastern North Pacific and is of questionable validity.

Dorsopsis taningi, characterized by large, dorsally directed eyes, is known only from the holotype (immature male, 15 mm ML). No additional specimens have turned up since the original description. The holotype was recently re-examined. The mantle is torn open dorsally and the head damaged. The right eye is popped out of its orbit and the optic stalk broken. The shape of both eyes is conspicuously distorted and flattened. The distribution of iridescence and pigmentation on the eyes is more consistent with laterally rather than dorsally directed eyes. The body proportions, especially the index of eye width to ML, do not differ significally from *Japetella.* On the basis of the above we concluded the genus *Dorsopsis* Thore, 1949 is a junior synonym of *Japetella* Hoyle, 1885.

Japetella Hoyle, 1885

GENERIC CHARACTERS.—*Adults:* Eyes relatively large, 10%-25% ML, narrowly separated (1 eye width); optic nerve stalk short, not detectable below 6 mm; digestive gland large,

nearly as long as mantle; iridophores present; gills with 8–11 lamellae per demibranch; hectocotylus present as enlarged suckers on right arm III. Monotypic.

Japetella diaphana Hoyle, 1885

SPECIES CHARACTERS.—*Adults* (Figure 241*a,b*): With characters of genus.

Eggs (Figure 241*c*): Unripe ovarian eggs, 1.2 × 0.2 mm (figured by Thore, 1949); larger eggs 3.0 × 1.0 mm (Robison and Young, 1981).

Young (Figure 241*d–g*): Hatchling stage unknown. Stage II larvae, 3.8 mm ML (Figure 241*e*): optic lobe abuts brain; eyes large, separated from each other by about 1 eye width; digestive gland situated anteriorly (i.e., esophagus abuts digestive gland <1/4 ML from anterior mantle margin); arms short, subequal with 4 suckers; arms with 2 chromatophores in single row; funnel clear; dorsal mantle clear; ventral mantle with 2 chromatophores on anterior margin; dorsal head with 8 chromatophores (2 + 6 pattern); 3 chromatophores over each eye; head with 2 chromatophores ventrally; dorsal surface of digestive gland with 6 viseral chromatophores (4 large + 2 small). Larvae of 12 mm ML: short optic stalk visible for first time; eyes separated by ~1.5 eye widths; esophagus abuts digestive gland ~1/3 ML from anterior mantle margin; arms with 5–6 suckers, largest on arms I.

GEOGRAPHICAL DISTRIBUTION.—Cosmopolitan in tropical to temperate waters.

VERTICAL DISTRIBUTION.—Lower mesopelagic to bathypelagic; 600 to 3000–4000 m; young (<25 mm ML) 100–330 m.

REMARKS.—*Japetella* larvae can be easily separated from other families whose larvae have transparent, sac-like bodies encased in a gelatinous coating. In the case of *Japetella* this jelly coat often appears "hairy" due to plankton debris that adheres to the coat. The body to arm ratio is 3 or 4:1. In side view, the eyes are oval and medium size with a large, centrally located lens. The digestive gland is large and ovoid. The beak is very small in comparison to larval vampyroteuthids. In dorsal view, the line from left eye through the brain to the right eye forms an angle and is not straight as in the vampyroteuthids.

REFERENCES.—Chun (1902, 1904, 1915), Clarke and Lu (1974, 1975), Green (1973), Herring et al. (1987), Joubin (1929, 1937), Lu and Clarke (1975b), Robson (1932a), Roper and Young (1975), Thore (1949), Young (1972a, 1978).

Eledonella Verrill, 1884

GENERIC CHARACTERS.—*Adults:* Eyes relatively small, 7%–11% ML, widely separated (2 eye widths); optic nerve stalk long, easily detectable; digestive gland 50% ML, situated well back from cephalic cone; iridophores absent; gills with 4–8 lamellae per demibranch; hectocotylus present as enlarged suckers on left arm III. Monotypic.

Eledonella pygmaea Verrill, 1884

SPECIES CHARACTERS.—*Adults* (Figure 242*a,b*): With characters of family.

Eggs (Figure 242*c*): Mature ovarian and oviducal eggs 2.0 × 1.3 mm (described and figured by Thore, 1949); mature ovarian egg 1.2 × 0.2 (figured under name *Bolitaena microcotyla* by Young, 1972b).

Young (Figure 242*d,e*): Hatchlings of 2 mm ML: described and figured by Young (1972b). Stage II larvae of 3.9 mm ML (Figure 243*e*): long optic stalk separates optic lobe from brain; eyes small, separated from each other by about 3 eye widths; digestive gland situated posteriorly (i.e., esophagus abuts digestive gland nearly 1/2 ML from anterior mantle margin); arms short, subequal with 4 suckers; chromatophore pattern incompletely known, appears to be as follows: ventral arms with 1 chromatophore, all other arms with 2 chromatophores in single row; funnel clear; dorsal mantle with 16–18 chromatophores (3–4 across); ventral mantle with band of 14–16 chromatophores on anterior margin; dorsal head with 8 chromatophores (4 + 4 pattern, 4 over brain and 2 each over optic lobe); no chromatophores over eyes; ventral head clear; dorsal surface of digestive gland with 6 visceral chromatophores (all small).

GEOGRAPHICAL DISTRIBUTION.—Cosmopolitan in tropical to temperate waters.

VERTICAL DISTRIBUTION.—Similar to *Japetella*.

REFERENCES.—Chun (1904, 1915), Naef (1928), Robson (1932a), Thore (1949), Young (1972b).

Family VITRELEDONELLIDAE Robson, 1930

FAMILY CHARACTERS.—*Adults:* Suckers uniserial, widely spaced; body sac-like, semigelatinous; mantle opening single, wide; tip of left arm III hectocotylized, not detachable; radula heterodont; long, slender digestive gland located posterior to stomach; eyes small, rectangular, directed laterally; inner demibranch of gills absent; funnel organ V-shape; mantle locking-apparatus absent; shell vestige absent. Monotypic.

Vitreledonella Joubin, 1918

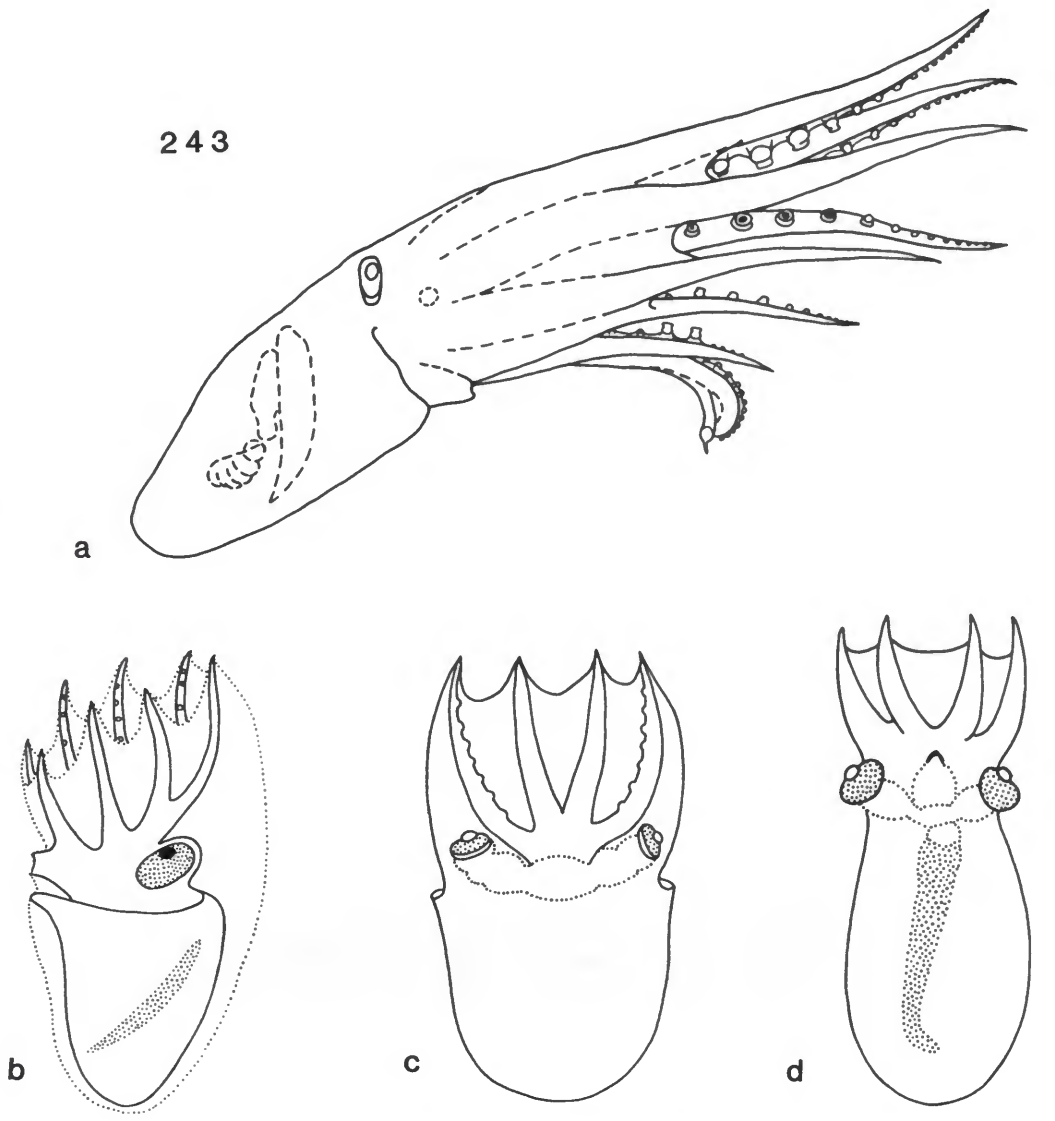
GENERIC CHARACTERS.—*Adults:* With characters of family. Monotypic.

Vitreledonella richardi Joubin, 1918

SPECIES CHARACTERS.—*Adults* (Figure 243*a*): With characters of genus.

Eggs: Mature eggs not known. Immature ovarian eggs elongate, 3.8 × 0.7 mm ML (figured by Thore, 1949). Said to hatch below 1000 m, possibly viviparous as 540 larvae taken with an adult female (Joubin, 1937; Thore, 1949).

Young (Figure 243*b–d*): Body encased in jelly-like coating; chromatophores uniformly present over entire body, small



FIGURES 243.—Vitreledonellidae, *Vitreledonella richardi*, central North Pacific: *a*, lateral view, adult male, 100 mm ML (R.E. Young, original); *b*, lateral view, hatchling, 2.2 mm ML; *c*, dorsal view, hatchling, 2.5 mm ML (*b,c*, redrawn from Joubin, 1937); *d*, dorsal view, young, 8 mm ML (original).

and inconspicuous, without pattern except for narrow band on ventral mantle composed of long, thin chromatophores; body to arm ratio 2:1 in "larvae" up to 11 mm ML; deep web connects all arms; 7 suckers present in single row on arms of 2.0–2.5 mm ML hatchlings, 10–11 suckers present by 11 mm ML; eyes of "larval" stages characteristically small, rectangular in shape in side view, and deeply pigmented in contrast to translucent body; digestive gland conspicuous, very long and slender (extends entire length of mantle), with slight turn at pointed posterior end; beak very small and translucent, darkened only on oral edge.

GEOGRAPHICAL DISTRIBUTION.—Cosmopolitan, in tropical to temperate waters.

VERTICAL DISTRIBUTION.—Mesopelagic to bathypelagic; adults >100 mm ML occur below 1000 m; larvae <11 mm ML in upper few hundred meters. Animals over 20 mm ML descend to greater depths.

REFERENCES.—Clarke and Lu (1974, 1975), Joubin (1918,

1920, 1924, 1929, 1937), Lu and Clarke (1975a, 1975b) Robson (1932a), Roper and Young (1975), Thore (1949).

Family ALLOPOSIDAE Verrill, 1882

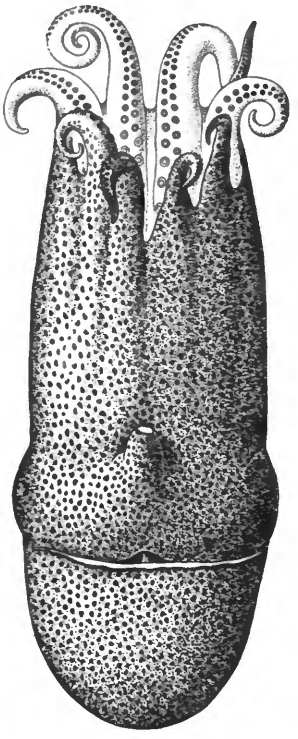
FAMILY CHARACTERS.—*Adults:* Suckers uniserial proximally, biserial distal to edge of web; web deep between all arms; body short, gelatinous, densely pigmented; mantle opening wide; funnel embedded in gelatinous tissue; radula heterodont; eyes large, diameter about 40% ML, hemispherical; entire right arm III hectocotylized, develops in pouch in front of eye, detachable; mantle locking-apparatus distinct, well developed; funnel organ W-shape; shell vestige absent. Monotypic.

Alloposus Verrill, 1880

GENERIC CHARACTERS.—*Adults:* With characters of family. Monotypic.

Alloposus mollis Verrill, 1880

SPECIES CHARACTERS.—*Adults* (Figure 244): With characters of the genus.



244

FIGURE 244.—Alloposidae, *Alloposus mollis*, ventral view, adult female, 70 mm ML, western North Atlantic. (From Verrill, 1881.)

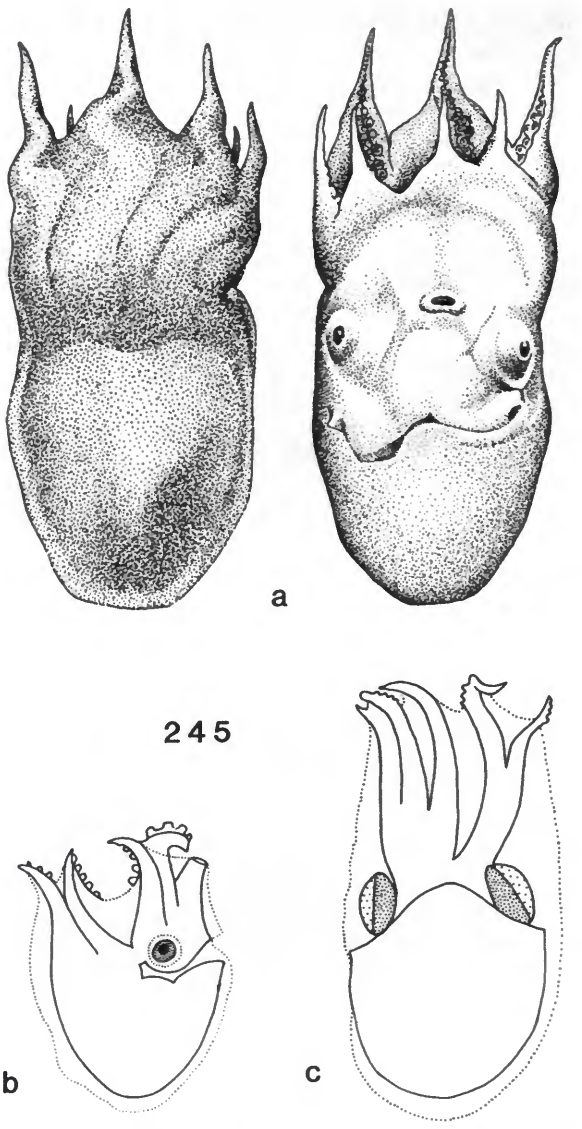


FIGURE 245.—Alloposidae, *Alloposus mollis*: *a*, dorsal and ventral views, male, 20 mm ML, eastern South Atlantic (from Adam, 1952); *b*, lateral view, young, 5.2 mm ML, North Atlantic (redrawn from Joubin, 1929); *c*, dorsal view, young, 9 mm ML, eastern North Atlantic (redrawn from Thore, 1949).

Eggs: Mature eggs not known. Immature ovarian eggs measure 1.5 × 0.5 mm, may be stalked when ripe (Thore, 1949).

Young (Figure 245): Body short, stubby, gelatinous; uniformly pigmented with small chromatophores; mantle to arm ratio about 1:1; eyes large and hemispherical; sucker arrangement and web as in adults.

GEOGRAPHICAL DISTRIBUTION.—Cosmopolitan in tropical and subtropical waters.

VERTICAL DISTRIBUTION.—Habits poorly known; possibly pelagic as young and benthic as adults (R.E. Young, pers.

comm.). Young caught in upper few hundred meters mostly near land masses (Thore, 1949).

REMARKS.—The 2.5 mm ML larva figured by Nesis (1979) and identified as *Alloposus* is now known to represent a young larva of *Tremoctopus*.

According to Kristensen and Knudsen (1983) and Willassen (1986) *Alloposus mollis* is a junior synonym of *Haliphron atlanticus* Steenstrup, 1859. According to convention the family name must also be changed to Haliphronidae (see Article 39, International Code of Zoological Nomenclature). The above synonymy has not been widely publicized and the family name change has not been proposed to the ICZN Commission. The name *A. mollis* currently is used by the majority of cephalopod researchers and has been consistently used since 1880. In order to avoid confusion, we concur with convention and retain the currently accepted *Alloposus mollis*.

REFERENCES.—Adam (1952), Alvarino and Hunter (1981), Hoyle (1886), Joubin (1929, 1937), Kristensen and Knudsen (1983), Lu and Clarke (1975a, 1975b), Lu and Roper (1979), Robson (1932a), Roper and Young (1975), Thore (1949), Tippmar (1913), Willassen (1986).

Family TREMOCTOPODIDAE Tryon, 1879

FAMILY CHARACTERS.—*Adults:* Cephalic water pores present, dorsal and ventral pairs; suckers biserial, small, numerous, widely spaced; arms I and II greatly elongate; web very deep dorsally, nearly absent ventrally; body thick and muscular in one species, gelatinous in second rarer species; sexual dimorphism pronounced, males dwarf; entire right arm III hectocotylized, develops in pouch below eye, detachable at maturity; radula heterodont; mantle locking-apparatus well developed; funnel organ a series of ridges; shell vestige present. Monotypic.

Tremoctopus Chiaje, 1830

GENERIC CHARACTERS.—*Adults:* With characters of family.

Tremoctopus violaceus Chiaje, 1830

SPECIES CHARACTERS.—*Adults* (Figure 246*a,b*): Body firm, muscular; color blue-purple dorsally, gold ventrally; gills with 13–16 lamellae per outer demibranch in females, 9–11 in males.

Eggs: Lays large masses consisting of more than 100,000 eggs (Hamabe, 1973); eggs measure 3.0–3.6 × 1.8–2.1 mm; egg stalks cemented together to form rod-like structures; rods of eggs held by suckers of dorsal arms where they are brooded (Naef, 1923).

Young (Figures 246*c–e*, 247, 248): Hatchlings, < 2 mm ML: translucent, cuff-shape brachial membrane envelops head and arms (skirt very similar to that of smallest larvae of *Argonauta*); long dorsal arms with very large suckers but without flaps or membranes at tips; single row of chromatophores extends along arms; hectocotylus visible. Larvae of 3–15 mm ML: body typically triangular in shape; web begins to form between the dorsal arms by 10 mm ML; dorsal mantle densely patterned with chromatophores; ventral mantle patterned with a band of 4–6 chromatophores along anterior margin; distinct, dense cluster of chromatophores posteriorly; chromatophores absent on mid-ventral mantle and on funnel; second row of chromatophores present on distal end of arms and single large chromatophore present on inner edge of each sucker; eyes large, surrounded by gold iridophores; males mature by 13–15 mm ML; mantle locking-apparatus well developed and conspicuous at all sizes.

Note: Larvae and young up to 15 mm ML usually hold pieces of *Physalia* (Portuguese-Man-of-War) tentacles in arms I and II. The suckers also are often filled with batteries of *Physalia* nematocysts (Jones, 1963).

GEOGRAPHICAL DISTRIBUTION.—Cosmopolitan in tropical, subtropical, and temperate seas.

VERTICAL DISTRIBUTION.—Epipelagic, to upper mesopelagic; surface to 300 m.

REMARKS.—According to Thomas (1977), *T. violaceus* consists of two subspecies. Comparisons of larvae have not been made and hence it is not known if this division can be resolved in early "larval" stages.

REFERENCES.—Adam (1937), Clarke and Lu (1975), Hamabe (1973), Jones (1963), Joubin (1902), Lu and Clarke (1975b), Naef (1923, 1928), Portmann (1937), Robson, (1932a), Roper and Young (1975), Sacarrao (1949, 1968), Tabeta (1969), Thomas (1977).

Tremoctopus gelatus Thomas, 1977

SPECIES CHARACTERS.—*Adults* (Figure 249*a*): Body gelatinous, transparent; eyes very large; water pores reduced in size; color light reddish brown; gills with 8–11 lamellae per outer demibranch in females, 7–8 in males.

Eggs: Not known.

Young (Figure 249*b,c*): Hatchling stage unknown. Young 2.5 mm ML: thick gelatinous layer covering thin mantle; Koelliker's bristles conspicuous; translucent, cuff-shape brachial membrane envelops head and arms; dorsal arms long, with large suckers.

GEOGRAPHICAL DISTRIBUTION.—Cosmopolitan in tropical and temperate seas.

VERTICAL DISTRIBUTION.—Mesopelagic; to 500 m.

REMARKS.—A rare species about which little is known. Specimen illustrated by Nesis (1979) probably belongs to this species.

REFERENCES.—Nesis (1979), Thomas (1977).

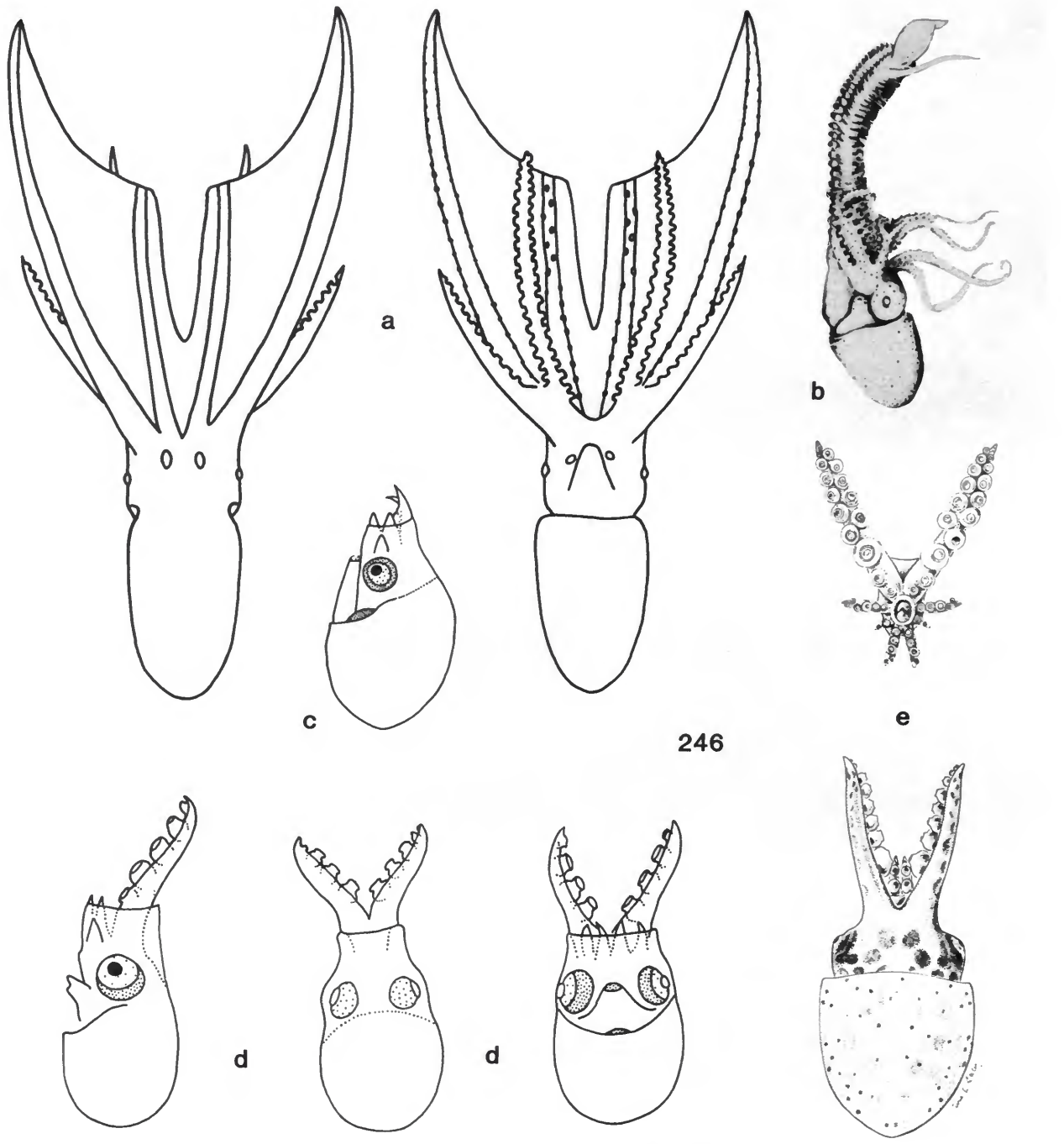


FIGURE 246.—Tremoctopodidae, *Tremoctopus violaceus: a,* dorsal and ventral views, adult female, 161 mm ML, North Atlantic (redrawn from Thomas, 1977); *b,* lateral view, adult male with hectocotylus extended, 17 mm ML, North Atlantic (from Joubin, 1937); *c,* lateral view, hatchling, 1.5 mm ML, Mediterranean (redrawn from Naef, 1923); *d,* lateral, dorsal, and ventral views, young, 2 mm ML, North Atlantic (Nixon original); *e,* dorsal and oral views, young, 2.2 mm ML, North Atlantic (Vecchione original).

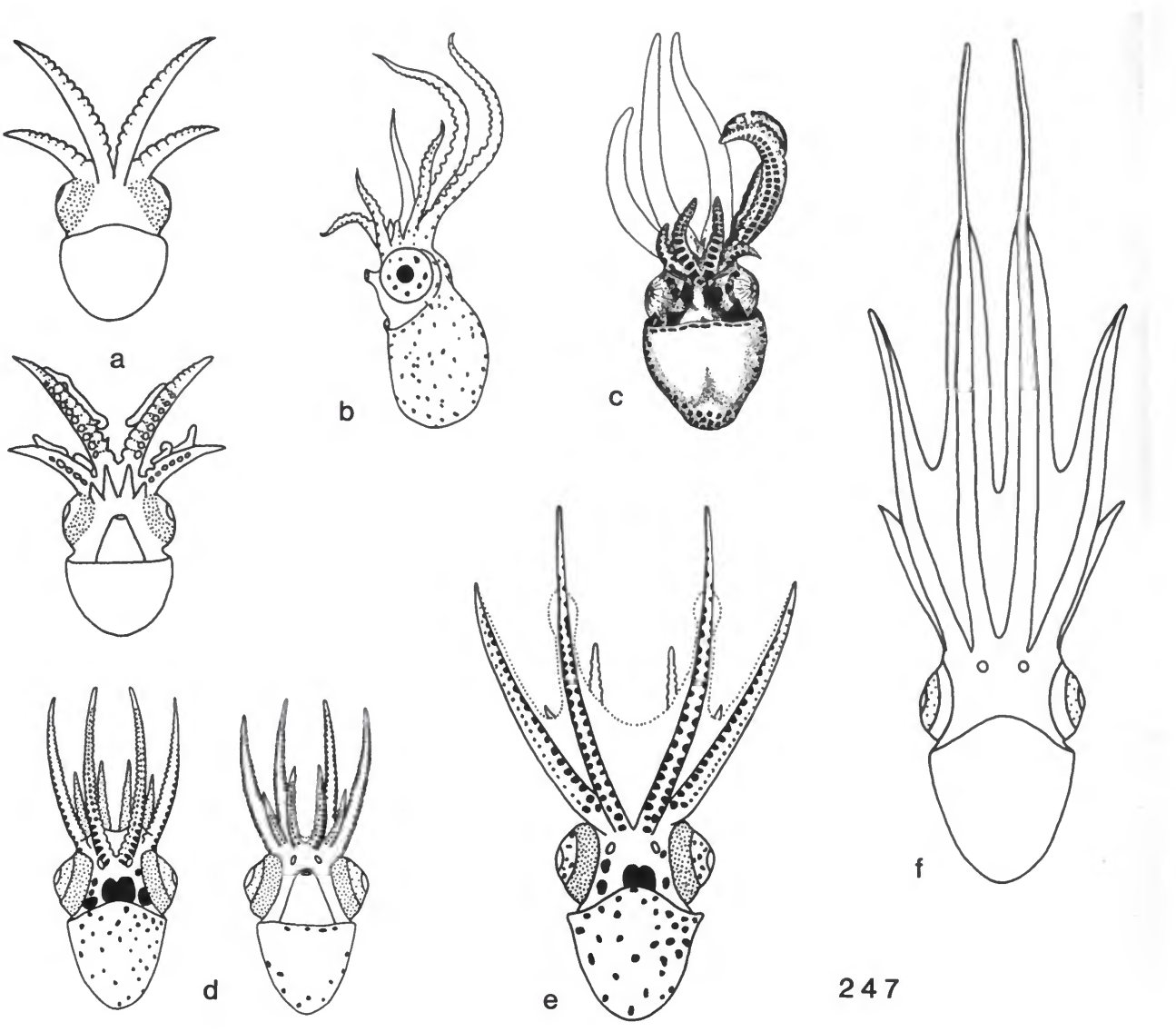


FIGURE 247.—Tremoctopodidae, *Tremoctopus violaceus*, female growth and development: *a*, dorsal and ventral views, young, 4 mm ML, Mediterranean (redrawn from Naef, 1923); *b*, lateral view, young, 5 mm ML, Mediterranean (redrawn from Chun, 1915); *c*, ventral view, young, 5.3 mm ML, North Atlantic (from Joubin, 1902); *d*, dorsal and ventral views, young, 6.7 mm ML, North Atlantic (redrawn from Thomas, 1977); *e*, dorsal view, young, 10.0 mm ML, North Atlantic (redrawn from Thomas, 1977); *f*, dorsal view, juvenile, 16 mm ML, Mediterranean (redrawn from Naef, 1923).

Family OCYTHOIDAE Gray, 1849

FAMILY CHARACTERS.—*Adults:* Suckers biserial; web nearly absent between all arms; body firm, thick, muscular; ventral mantle surface of females patterned with tubercles and ridges in reticulate pattern; gills, 19-20 lamellae per demibranch; sexual dimorphism pronounced, males dwarf, often residing in pallial chamber of pelagic salps; females large at maturity (up to 300 mm ML); entire right arm III hectocotylized, develops within stalked pouch, detachable when males mature; radula heterodont; funnel long, extends anterior to base of arms; mantle locking-apparatus well developed, complex;

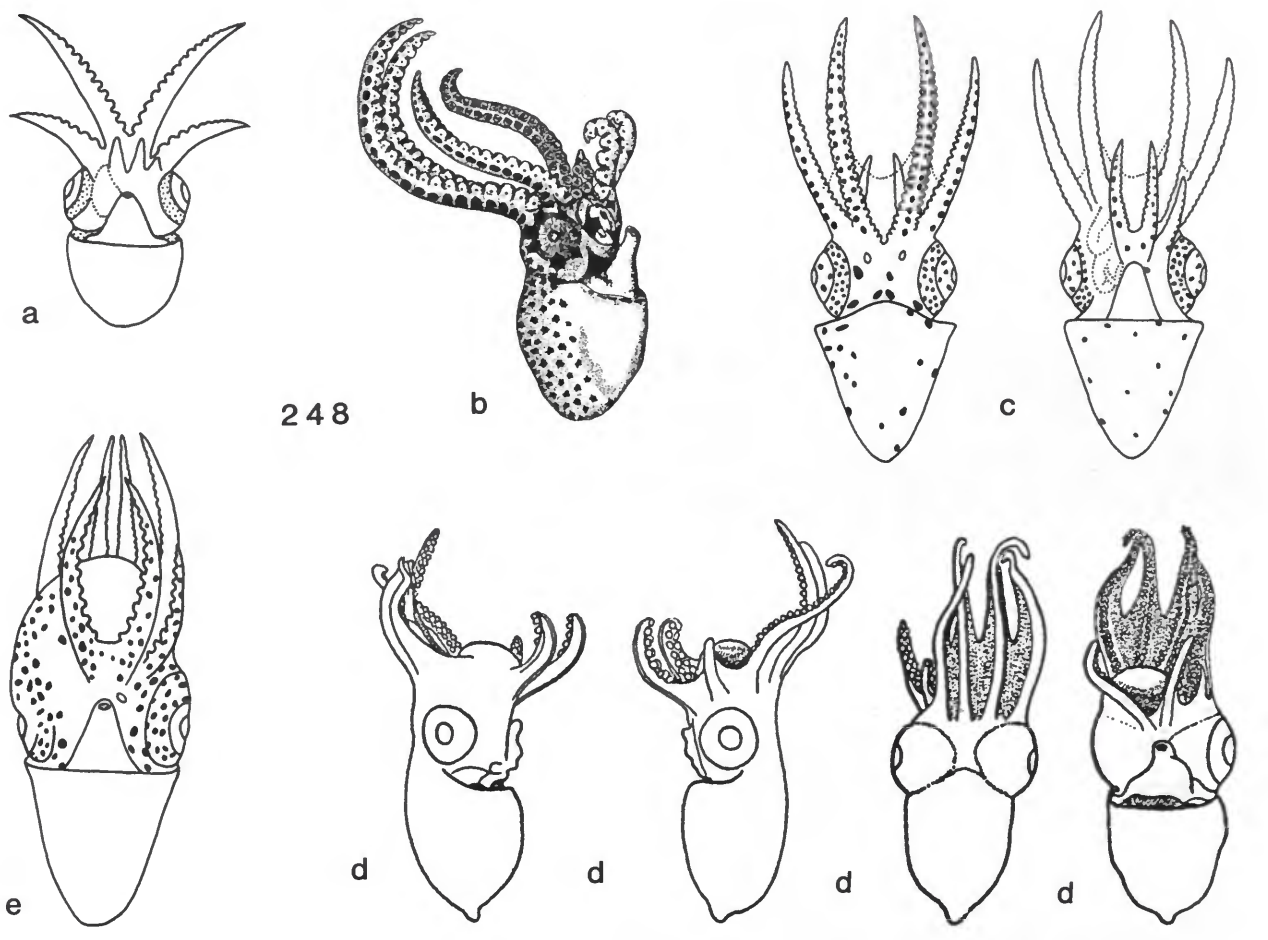


FIGURE 248.—Tremoctopodidae, *Tremoctopus violaceus*, male growth and development: *a*, ventral view, young, 4 mm ML, Mediterranean (redrawn from Naef, 1923); *b*, lateral view, young, 6 mm ML, North Atlantic (from Joubin, 1902); *c*, dorsal and ventral views, young, 7.1 mm ML, North Atlantic (redrawn from Thomas, 1977); *d*, lateral, dorsal, and ventral views, immature male, 11 mm ML (from Adam, 1937); *e*, ventral view, adult male, 13.2 mm ML, North Atlantic (redrawn from Thomas, 1977).

arm pairs I and IV greatly elongate; single ventral pair of cephalic water pores present; shell vestige absent; funnel organ W-shape. Monotypic.

Ocythoe Rafinesque, 1814

GENERIC CHARACTERS.—*Adults:* With characters of family. Monotypic.

Ocythoe tuberculata Rafinesque, 1814

SPECIES CHARACTERS.—*Adults* (Figure 250*a–c*): With characters of genus.

Eggs: Apparently ovoviviparous; oviducts extremely long and convoluted in mature females, contain large number of eggs; embryonic development proceeds as eggs move along oviducts (Naef, 1923); mature ovarian eggs measure 1.75 × 1.0 mm; more than 100,000 eggs contained in ovary of mature females (Roper and Sweeney, 1976).

Young (Figure 250*d–h*): Distinctive at all sizes; head and arms of smallest larval stages not enclosed in cuff-shape brachial membrane (see *Tremoctopus* and *Argonauta*); distinctive arm length formula (arms I and IV greatly elongated) evident even in hatchlings; funnel long, extends well anterior to base of arms; reticulate pattern on ventral mantle of female

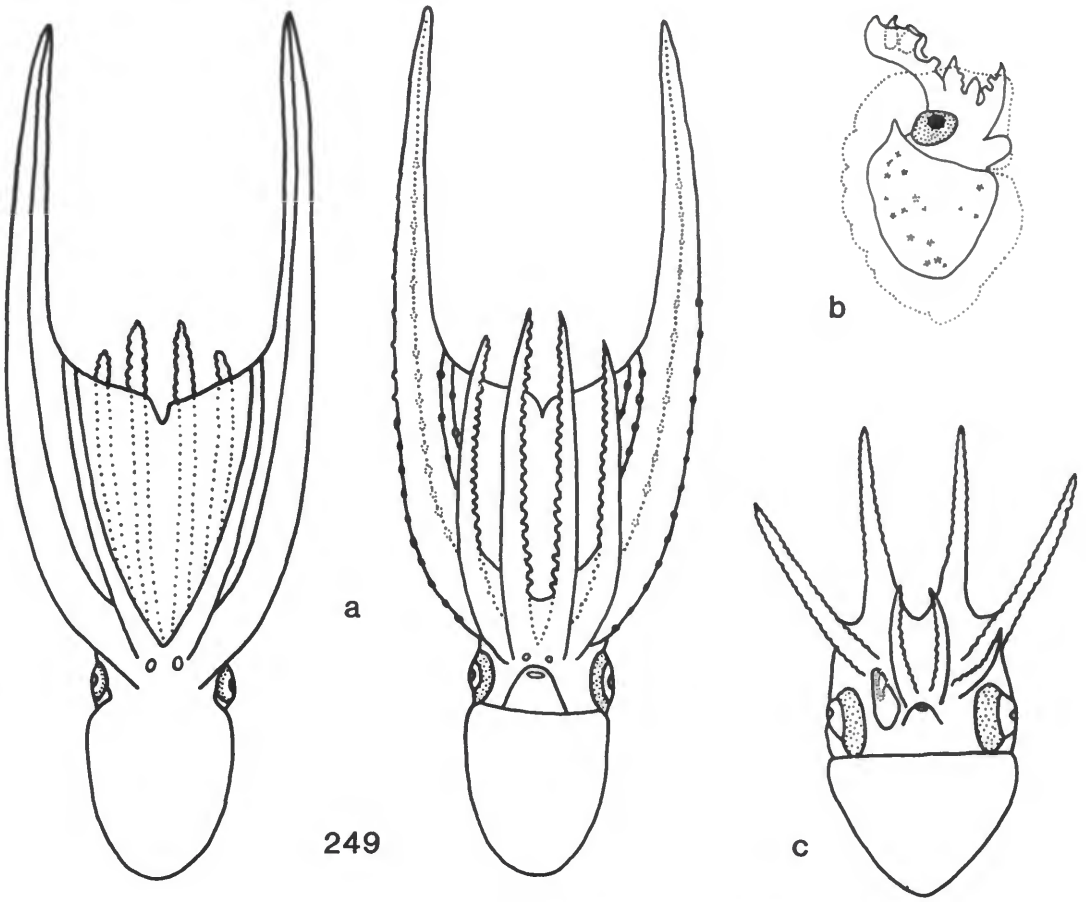


FIGURE 249.—Tremoctopodidae, *Tremoctopus gelatus: a,* dorsal and ventral views, adult female, 328 mm ML, western North Atlantic (redrawn from Thomas, 1977); *b,* lateral view, posthatchling, 2.5 mm ML (redrawn from Nesis, 1979); *c,* ventral view, immature male, 10 mm ML, central North Pacific (redrawn from Thomas, 1977).

evident in larvae as small as 10 mm ML; dorsal mantle of both sexes covered with uniform pattern of tiny chromatophores; ventral mantle of both males and females devoid of chromatophores; ventral water pores clearly evident at all stages.

GEOGRAPHICAL DISTRIBUTION.—Cosmopolitan in tropical to temperate seas.

VERTICAL DISTRIBUTION.—Epipelagic, surface to 200 m; young found in near surface waters.

REFERENCES.—Berry (1916), Jatta (1896), Joubin (1929), Naef (1923, 1928), Robson (1932a), Roper and Sweeney (1976), Sanchez (1980), Sasaki (1929).

Family ARGONAUTIDAE Tryon, 1879

FAMILY CHARACTERS.—*Adults:* Suckers biserial, on long stalks, borne on marginal membrane; web very shallow; body firm, mantle thin and muscular; distal tips of dorsal arms of females with broad, expanded, membranous, glandular flaps that secrete and hold secondary shell; sexual dimorphism pronounced, males dwarf; entire left arm III hectocotylized, develops in pouch beneath eye, autotomized when mature; female produces large, fragile external shell in which eggs are brooded; radula heterodont; mantle locking-apparatus well

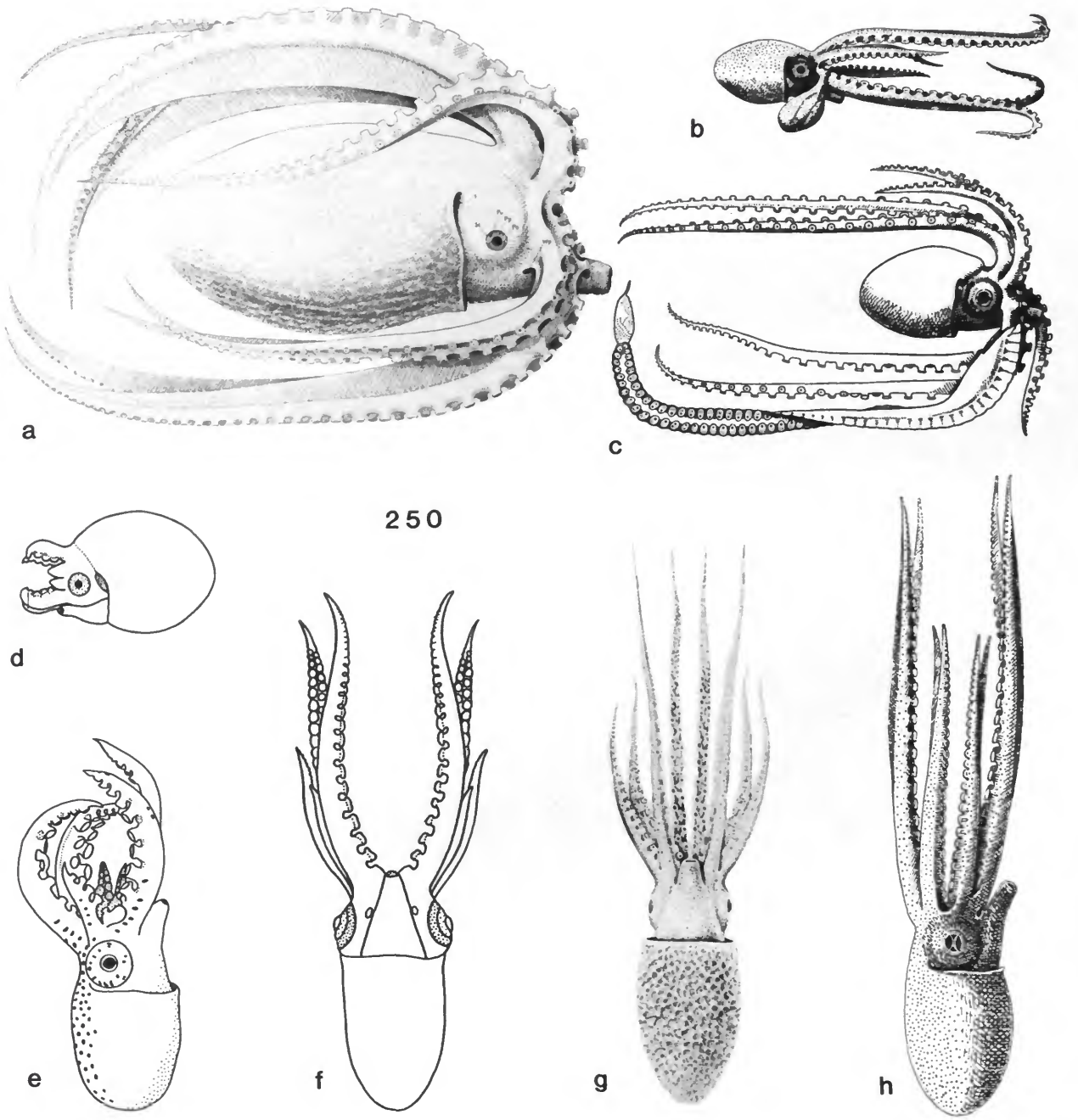


FIGURE 250.—Ocythoidae, *Ocythoe tuberculata: a,* lateral view, adult female, 270 mm ML; *b,* lateral view, adult male with hectocotylus enclosed in sac, 24 mm ML; *c,* lateral view, adult male with hectocotylus extended, 25 mm ML; *d,* lateral view, posthatchling, 2.3 mm ML; *e,* lateral view, young male, 4.5 mm ML, North Atlantic (redrawn from Joubin, 1929); *f,* ventral view, young female; *g,* ventral view, immature female showing reticulations on ventral mantle, eastern North Pacific (from Young, 1972a); *h,* lateral view, immature female, 25 mm ML. (*a–d,f,h,* from Mediterranean, after Naef, 1923; *d, f,* redrawn).

developed and complex; funnel organ W-shape; shell vestige absent. Monotypic.

Argonauta Linne, 1758

GENERIC CHARACTERS.—*Adults* (Figure 251*a–c*): With characters of family.

Eggs: Among smallest known for cephalopods (see Table 5).

Young (Figures 251*d–h*, 252): Larvae, other than hatchlings, completely covered with chromatophores, specific patterns not recognized; conspicuous cuff-shape brachial membrane surrounding arms of larvae <3.0 mm ML; mantle to arm ratio of larvae 2–5 mm ML, 2:1 or 3:1, approaches 1:1 in larvae >5 mm ML; membranous shell flaps on elongate dorsal arms of females detectable at >3 mm ML (dorsal arms of preserved female larvae often tightly coiled and reflexed over the head where their distinctive size and shape can be overlooked); external shells present in females at least by 8 mm ML depending on species; hectocotylus can be recognized in males as small as 1.5 mm ML; left third arm short, blunt, enveloped by conspicuous sac by 1.5 mm ML; epidermis in most preserved small larvae loose, translucent; funnel broad and short, extends only to anterior edge of eye in larvae <2 mm ML; mantle locking-apparatus well developed, conspicuous even in hatchlings. The locking-apparatus clearly separates larval argonautids from larval octopodids.

Note: Surprisingly little is known about reproduction and development in the argonauts considering that members of the family are so conspicuous and common. At present, it is not possible to separate larval stages to species. The presence of a conspicuous cuff-shape membrane surrounding the arms of larvae <3.0 mm ML facilitates recognition of argonauts in the plankton.

A single 6.5 mm ML male was found in which the hectocotylus was on the right side (Vecchione, pers. comm.). Whether this is an isolated instance or a species specific character is not known.

REMARKS.—Shells are found on beaches and in the stomachs of marine predators. Whole animals are rare in collections. Occasionally hundreds or even thousands of individuals from a swarm are blown ashore in mass strandings. Six species currently are recognized based primarily on differences in the "brood shell." Little information is available to differentiate these species on the basis of morphological features of adult males and females or larval stages. The following species are recognized: *Argonauta argo* Linne, 1758; *A. boettgeri* Maltzan, 1881; *A. cornuta* Conrad, 1854; *A. hians* Lightfoot, 1786; *A. nodosa* Lightfoot, 1786; *A. nouryi* Lorois, 1852. For keys to species see Nesis (1987), Robson (1932a), Sasaki (1929), and Voss (1955).

Argonauta argo Linne, 1758

SPECIES CHARACTERS.—*Adults* (Figure 251*a,b*): Females: arms IV longer than arms II and III; arms I with 150 suckers; gills with 28 lamellae per outer demibranch; shell compressed; center of spiral flat, auricles absent in large shells, may be present in young shells; 50+ lateral ribs, each terminating in nodule on keel; keel very narrow (6% of shell diameter) with numerous, small, acute nodules; color white with black or brown markings on early shell and keel. Males: hectocotylus with 65 suckers.

Eggs: Very small, 0.6–0.8 mm.

Young (Figures 251*h,i;* 252*e–i*): Prehatchling (stage XX) 0.85 mm ML (Figure 251*h,i*): described and figured by Fioroni (1978). Hatchling 0.75–0.9 mm ML (Figure 251*h,i*): conspicuous cuff-shape brachial membrane; eyes small, directed slightly anteroventrally; arms short, subequal with 3 suckers; arms with 1 chromatophore at base of brachial membrane; funnel with 2 + 2 chromatophores, dorsal mantle anterior and mid region clear, with 4 chromatophores in posterior cap; ventral mantle with 4–5 chromatophores on anterior margin, mid and posterior region clear; dorsal head with 2 chromatophores; 2 chromatophores dorsally over each eye; 1 chromatophore ventrally over eye; dorsal surface of digestive gland with 9–11 large visceral chromatophores. Later larval stages: developmental sequences for females and males described and figured by Naef (1928), and for males by Grimpe (1928). See also Sacarrao (1951a) and Fioroni (1978).

GEOGRAPHICAL DISTRIBUTION.—Cosmopolitan, subtropical to tropical coastal and oceanic waters.

VERTICAL DISTRIBUTION.—Epipelagic. Closing-net captures of *A. argo* were made off Bermuda (5–8 mm ML) at 50–200 m and in the Mediterrranean (5–13 mm ML) at the surface at night (Roper and Young, 1975).

REFERENCES.—Adam (1937), Boletzky (1983), Boletzky and Centelles (1979), Clarke and Lu (1975), Fioroni (1978), Grimpe (1928), Joubin (1892), Koelliker (1844), Lacaze-Duthiers (1892), Lu and Clarke (1975b), Mueller (1853), Naef (1923, 1928), Nishimura (1968), Okutani and Kawaguchi (1983), Robson (1932a), Roper and Young (1975), Sacarrao (1951a), Voss (1955), Voss and Williamson (1971), J.Z. Young (1960).

Argonauta boettgeri Maltzan, 1881

SPECIES CHARACTERS.—*Adults* (Figure 251*c,d*): Females: arms IV shorter than arms II and III; shell wide, surface finely granular; center of spiral depressed; auricles absent; 40–45 lateral ribs; keel well defined, wide (10%–15% of shell diameter), devoid of nodules; color white to ochre. Males: unknown.

Eggs: Small, 0.85–1.1 mm, ovoid with short stalk.

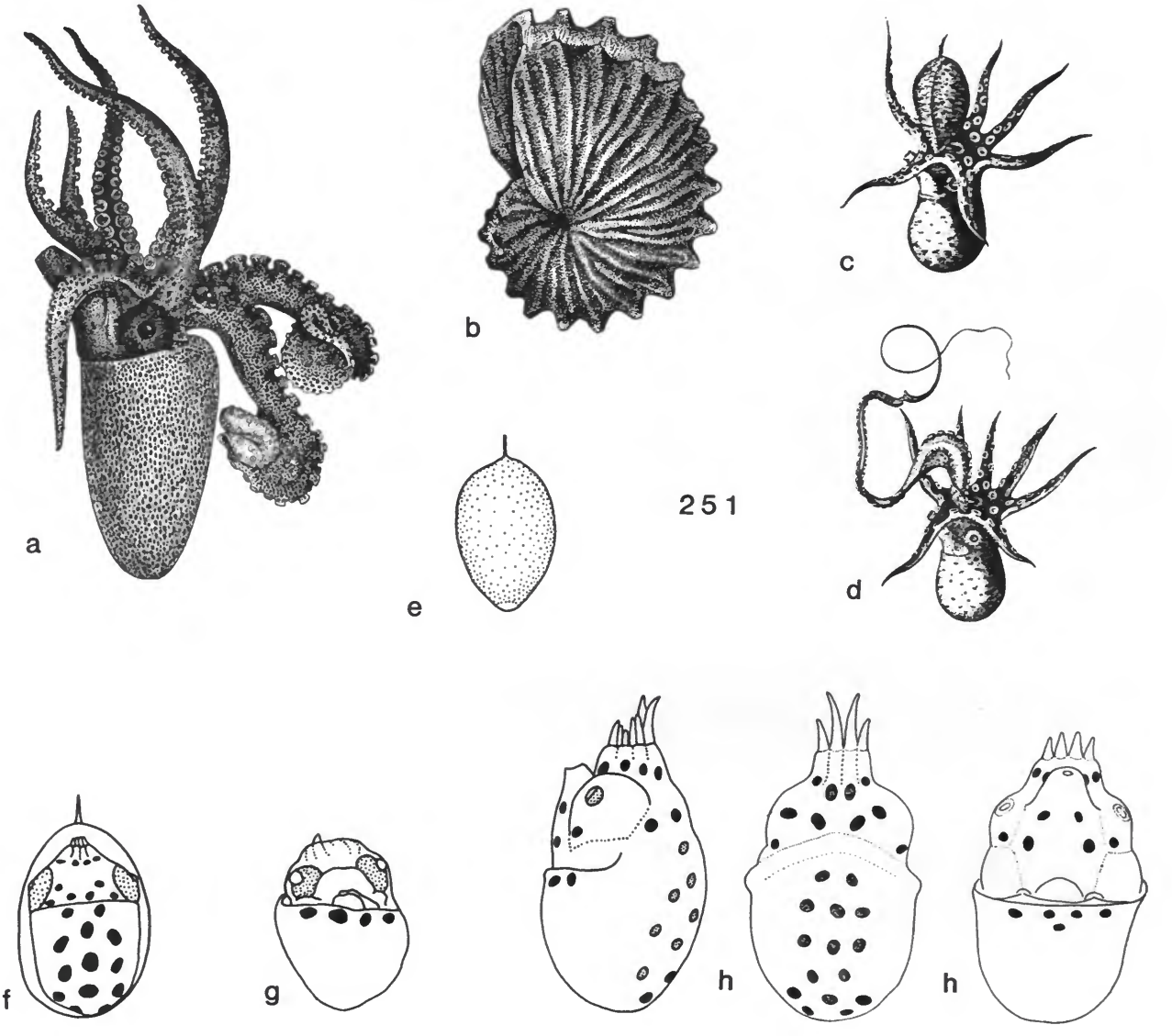


FIGURE 251.—Argonautidae: *a,b, Argonauta bottgeri: a,* lateral view, adult female out of shell, 22 mm ML, Hawaiian waters (from Berry, 1914); *b,* secondary shell of previous specimen. *c,d, Argonauta argo:* lateral view, adult male with hectocoylus enclosed in sac (*c*) and extended (*d*), Mediterranean (from Mueller, 1853). *e, f, Argonauta hians,* western Pacific (redrawn from Nesis, 1977): *e,* egg capsule, 1.1 mm CL (capsule length); *f,* dorsal view, fully developed embryo in egg capsule, 0.85 mm ML. *g, Argonauta* sp., ventral view, hatchling, 0.85 mm ML, western North Pacific (redrawn from Shojima, 1970). *h, Argonauta argo,* lateral, dorsal, and ventral views (bc = brachial cuff; clear circles = supravisceral chromatophores), hatchling, 0.9 mm ML, Mediterranean (lateral view redrawn from Fioroni, 1978; other views from Fioroni, 1965).

Females spawn every night; incubation lasts approximately 3 days; larvae released every night (Nesis, 1977).

Young: Hatchlings 1.05–1.25 mm ML: arms short, subequal with 3 suckers; chromatophore pattern similar to *A. argo;* arms with 1 chromatophore at arm base; dorsal mantle appears to be clear; dorsal head with 6 chromatophores in 2 + 4 pattern;

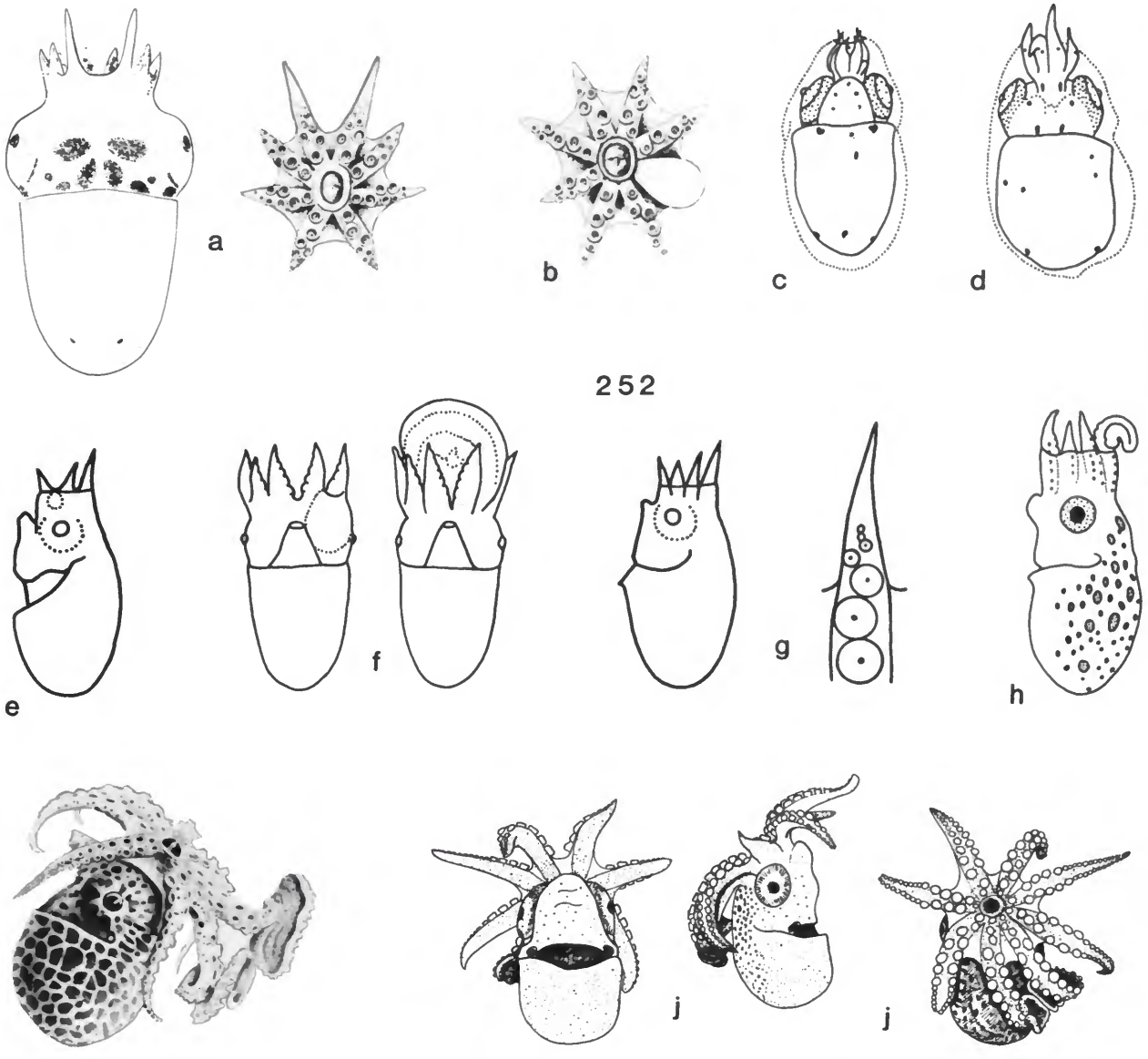


FIGURE 252.—Argonautidae: *a,b, Argonauta* sp., North Atlantic (Vecchione original): *a,* dorsal and oral views, young female, 1.8 mm ML; *b,* oral view, young male, 1.5 mm ML. *c,d, Argonauta hians,* eastern South Pacific (redrawn from Nesis, 1973): *c,* ventral view, young male, 1.8 mm ML; *d,* dorsal view, young male, 2.1 mm ML; *e–i, Argonauta argo,* Mediterranean (redrawn from Naef, 1923): *e,* lateral view, young male, 2.5 mm ML; *f,* ventral views, young males with small hectocotylus sac and with hectocotylus fully developed but still in sac, both 4 mm ML; *g,* lateral view and oral view of right arm III, young female, 2.5 mm ML; *h,* lateral view, young female with dorsal shell-producing arms differentiated, 4 mm ML; *i,* lateral view, young female, 5 mm ML. *j, Argonauta* sp., lateral, ventral, and oral views, young female, 9 mm ML (from Adam, 1937).

dorsal surface of digestive gland with 12–13 large visceral chromatophores. Later larval stages: females begin to build shells by 6.5–7 mm ML; mate at 12–13 mm ML; lay eggs by 15 mm ML. Males mature at 7 mm ML; die after first mating.

GEOGRAPHICAL DISTRIBUTION.—Indo-West Pacific, tropical and subtropical oceanic waters.

VERTICAL DISTRIBUTION.—Epipelagic.

REFERENCES. Berry (1914), Nesis (1973, 1977), Sasaki (1929).

Argonauta hians Lightfoot, 1786

SPECIES CHARACTERS.—*Adults:* Females: arms IV shorter than arms II and III; arm I with 60 suckers; gills with 20 lamellae per outer demibranch; shell wide, surface polished; center of spiral inflated, auricle present *or* absent; 30–35 lateral ribs, every other one terminating in nodule on keel; keel wide with prominent, rounded, widely spaced nodules; color whitish yellow to light brown on keel. Males: hectocotylus with 45–50 suckers.

Eggs: Small, 0.7–0.8 mm. Females spawn every night, therefore eggs in shell in different stages of development; incubation lasts approximately 3 days; larvae released every night.

Young: Hatchling stages unknown, thought to be <1 mm ML. Later stages resemble developmental pattern described for *A. boettgeri.*

GEOGRAPHICAL DISTRIBUTION.—Cosmopolitan, tropical oceanic waters. Absent from Mediterranean.

VERTICAL DISTRIBUTION.—Epipelagic. Larvae are very lively and appear to undergo limited vertical distribution. Larvae actively school during the day but disperse at night when they move into surface waters.

REFERENCES.—Kubota and Miyashita (1973, 1975), Nesis (1972, 1973, 1977), Sasaki (1929), Voss (1971).

Argonauta sp.

SPECIES CHARACTERS.—*Young:* Hatchling 0.8 mm ML (Figure 251*g*), figured by Shojima (1970). Later larval stages (Figure 252*a,b,j*), figured by Vecchione (original) and Adam (1937), could not be identified to species. See also Voss (1971).

Family OCTOPODIDAE Orbigny, 1840

FAMILY CHARACTERS.—Body muscular to gelatinous; suckers uniserial *or* biserial; radula heterodont, occasionally homodont; digestive gland anterior to stomach and caecum; crop present, well developed, poorly developed, *or* absent, crop diverticulum present or absent; hectocotylus present, large and spoon-shape to minute and nearly smooth, end organ on tip of right *or* left arm III, not autotomized at maturity; mantle locking-apparatus absent; ink sac present, vestigial, *or* absent; light organs absent; shell vestige present in some species as a pair of cartilage-like (conchiolin) stylets in mantle; Koelliker's bristles present *or* absent in young; functional chromatophores of several colors present.

SUBFAMILY CHARACTERS.—The octopodids traditionally have been divided into 3 subfamilies: Octopodinae, Bathypolypodinae, and Eledoninae. Voss (1988a) redefined the subfamilies and added a fourth, the Graneledoninae.

GENERIC CHARACTERS (Figure 253).—The Octopodidae is the largest and most important family of octopods and one of the 4 most important families of cephalopods in regard to current and potential fishery exploitation. Voss (1977) lists 25 nominal genera in the family. In total, well over 200 species have been described. Generic and species boundaries are often unclear. A number of genera and many species have been erected on the basis of insufficient or unsuitable material. A study of character variability and generic classification in the octopodines currently is being conducted by R.B. Toll.

Eggs and Young: Octopodid eggs are all similar, with a sausage- or pear-shape capsule (chorion) and a stalk of varying length (Boletzky, 1986). The majority of species of octopuses attach their eggs to the substrate by means of the stalk. Depending on the species, the eggs are either attached singly (Figure 254*a,b*) or the stalks are entwined and the eggs attached in clusters or festoons (Figure 254*c*). In most species females spawn only once. Females remain with the eggs to brood and groom them throughout the developmental period, after which the females die. In a few cases (i.e., *Octopus burryi, Hapalochlaena maculosa,* and an undescribed species in Hawaiian waters) the eggs are carried and brooded loose in the web of the female (see Forsythe and Hanlon, 1985; Dew, 1959; Tranter and Augustine, 1973).

Egg capsules of the octopodids range in length from 1.5–35.0 mm. Eggs over 10.0 mm capsule length produce crawl-away, demersal young. Eggs in the lower end of the range, 1.5–5.0 mm, give rise to planktonic larvae. Intermediate-size eggs, 6.0–9.0 mm, produce either planktonic or benthonic hatchlings depending on the specific egg index. Brood or clutch size is dependent on the relative volume of the body of the female. Small egg species spawn a greater number of eggs per body weight than large egg species. Table 6 lists information on egg capsule length, egg number, and habits of young for a diversity of octopodids.

REMARKS.—The Octopodinae is the largest contributor to the planktonic octopod fauna. Hatchlings of species with planktonic larvae measure 2.0–8.0 mm ML and are characteristically covered with Koelliker's bristles (Figure 254*d*). The eyes are large and prominent. The arms typically are short and stubby but in some species they taper to delicate thread-like tips beyond the sucker-bearing part. Typically only a few suckers (3–4) are present in a single, straight row. The mantle is generally short and rounded. The ratio of ML to AL (arm length) is in the range from 3:1 to 2:1. During growth in the plankton or at the time of settlement, the bristles are lost, the arms elongate, suckers are added, and the mantle grows longer until the young begin to resemble the adults. Hatchlings from small eggs swim to near surface waters where they develop for a period of time until ready to settle. Marliave (1981) postulated that larvae of one species, *O. dofleini,* attach to the surface film. In aquaria they appear to get trapped to the surface film. Nothing comparable to metamorphosis occurs prior to

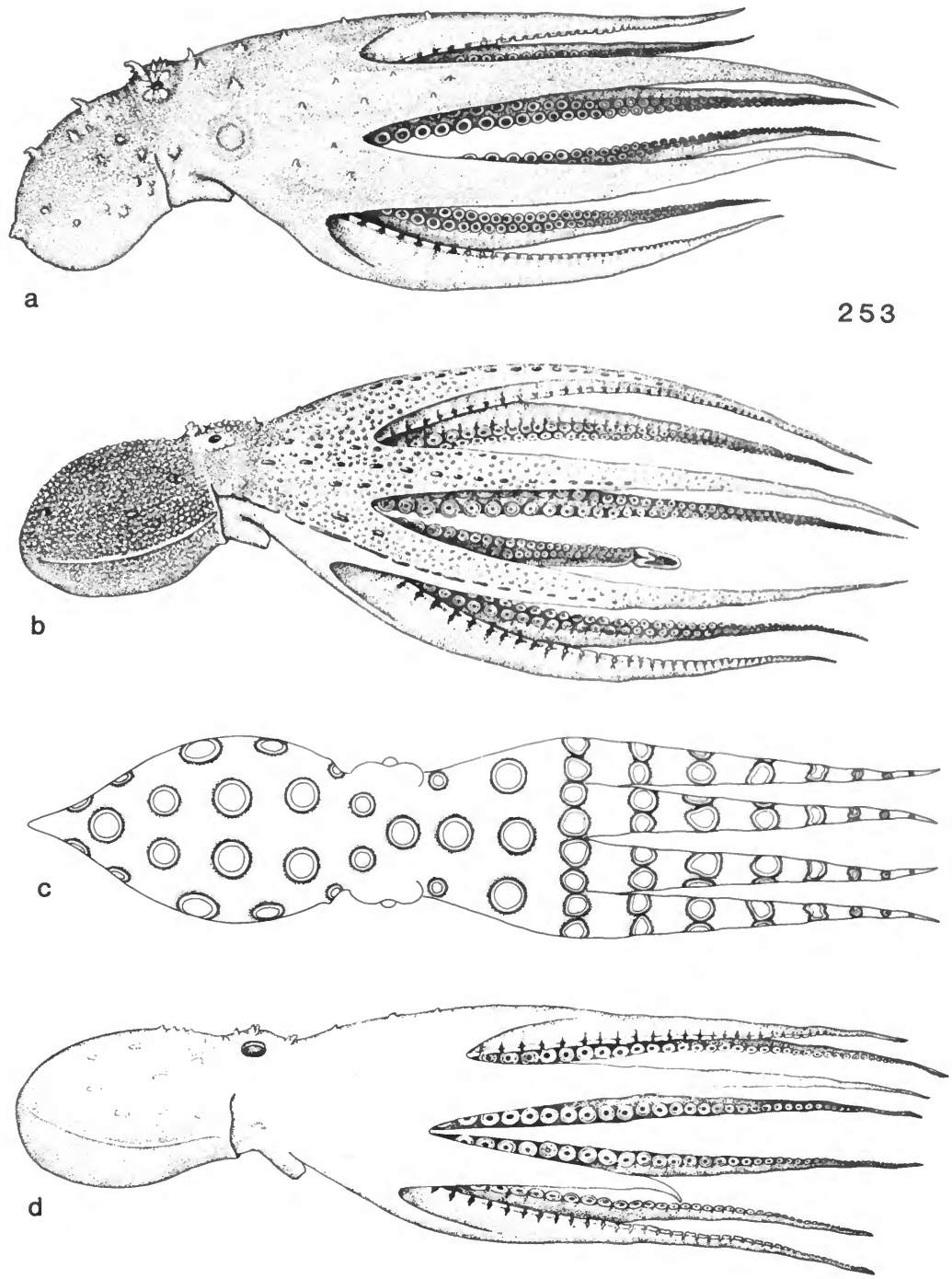


FIGURE 253.—Octopodidae: *a, Octopus hummelincki,* lateral view, adult male, Caribbean (from Palacio, 1977); *b, Scaeurgus unicirrhus,* lateral view, adult male, 50 mm ML, Mediterranean (from Palacio, 1977); *c, Hapalochlaena lunulata,* dorsal view, adult female, 40 mm ML, Indo-Pacific (off Australia) (from Roper and Hochberg, 1988); *d, Eledone cirrhosa,* lateral view, adult male, Mediterranean (from Palacio, 1977).

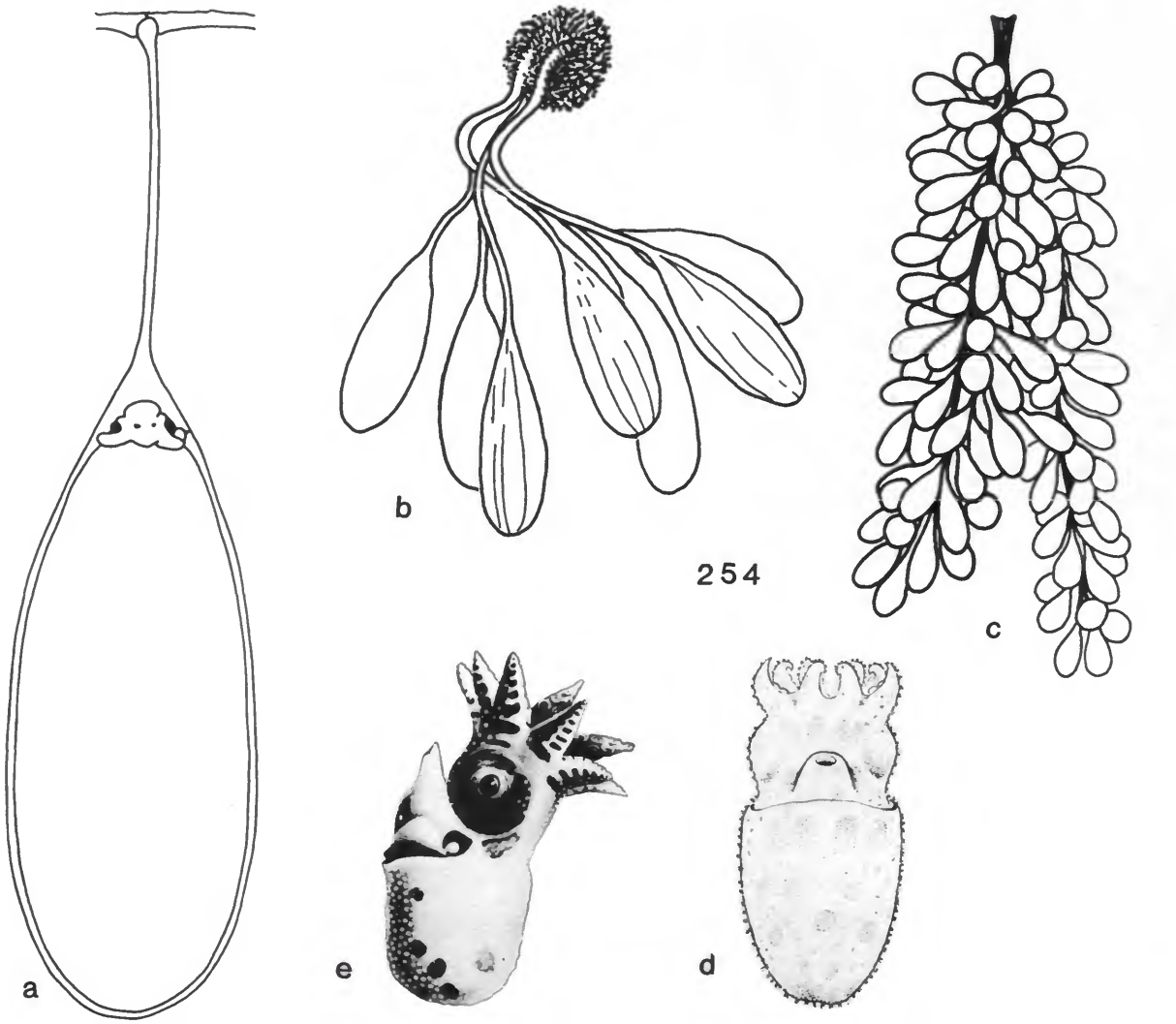


FIGURE 254.—Octopodidae, *Octopus* eggs and hatchlings: *a*, *Octopus conispadiceus*, large egg species, 18 mm CL (capsule length), egg attached individually to substrate, western North Pacific (redrawn from Ito, 1983); *b*, *Eledone cirrhosa*, intermediate size egg species, 7 mm CL, eggs cemented to substrate in small clusters, Mediterranean (redrawn from Fioroni, 1978); *c*, *Octopus* cf. *vulgaris*, small egg species, 2.5 mm CL, eggs attached in festoons or strings to substrate, Mediterranean (redrawn from Fioroni, 1978); *d,e*, *Octopus* cf. *vulgaris*, recent hatchling covered with Koelliker's bristles: *d*, ventral view, 2.6 mm ML, English Channel (from Rees, 1953); *e*, lateral view, 3.0 mm ML, Mediterranean (from Chun, 1915).

settling. The length of the planktonic phase is unknown, but based on laboratory reared *O. vulgaris* it is thought to be limited to a few weeks or at most a few months. Most young probably settle out at between 6.0–10.0 mm ML. However, in at least a few species young grow to considerable size in the plankton (i.e., *O. burryi*, 15.0 mm ML; *O. dofleini*, 14.0 mm ML; *O. ornatus*, 16.0 mm ML; *O. rubescens*, 19.0–25.0 mm ML). The first thorough description of the development and planktonic larval stages of the octopodids is found in Naef (1923, 1928). At present, only a few species have been studied in detail. Those that have been described in complete detail and that can be used as models to document, describe, and compare other species are indicated in the species accounts by asterisks (*). A number of additional observations and figures are

TABLE 6.—Egg size, egg number, and habits of hatchlings in the Octopodidae (†, in species column, larval stages figured in this chapter; *, mature ovarian eggs; A, Atlantic Ocean distribution; B, crawl away juveniles; I, Indian Ocean distribution; IWP, Indo-West Pacific distribution; P, in habits column, planktonic larval stage; P, in distribution column, Pacific Ocean distribution).

Species	Length of egg capsule (mm)	Egg number	Habits of hatchlings	Geographical distribution	Reference
		SMALL EGG SPECIES WITH LONG DURATION PLANKTONIC LARVAE			
Octopus aegina	2.0	-	P	IWP to Red Sea	Eibl-Eibesfeldt and Scheer (1962)
O. alecto	2.0–2.5	-	P	Gulf of California	Hochberg (unpub.)
O. berenice	1.5	-	P	South Pacific	Pickford and Townsley (unpub.)
†*O. bimaculatus*	2.5–4.0	20,000	P	P-USA, Mexico	Ambrose (1981); Pickford and McConnaughey (1949)
O. brocki	1.5–2.0	-	P	South Pacific	Pickford and Townsley (unpub.)
†*O. burryi*	2.2–2.5	35,000	P	A-Amphitropical	Forsythe (1984b); Voss (1951b)
†*O. cyanea*	2.0–3.0	110,000–700,000	P	P-Hawaii–Australia	LeSouef and Allen (1933, 1937); Van Heukelem (1973, 1976, 1983a)
†*O. defilippi*	1.5–2.1	10,000+	P	A-Amphitropical	Naef (1928)
O. duplex	2.0–2.5	-	P	Australia	Hochberg and Lu (unpub.)
O. hawaiiensis	3.0	2,000–4,000	P	P-Hawaii	Houck (1977); Hochberg (unpub.)
O. hummelincki	2.0–3.0	-	P	A-Caribbean	Burgess (1966); Voss (1975)
O. luteus	3.4	-	P	P-Japan	Arakawa (1962a, 1962b); Sasaki (1929)
†*O. macropus*	1.5–2.0	-	P	A-Amphitropical	Naef (1923, 1928); Robson (1929b); Voss and Phillips (1957)
O. membranaceus	1.5–3.0	-	P	Australia	Hochberg and Lu (unpub.); Okutani et al. (1987)
†*O. ornatus*	2.0–3.0	-	P	P-Hawaii	Young et al. (1989)
O. ovulum	2.0–3.0*	-	P	P-Japan	Sasaki (1917b, 1929)
O. parvus	1.8*	-	P	P-Japan	Sasaki (1929)
†*O. rubescens*	3.0–4.0	4,000–45,000	P	P-Alaska to Mexico	Dorsey (1976); Fisher (1923); Green (1973); Hochberg and Fields (1980); MacGinitie and MacGinitie (1968)
O. selene	1.0*	-	P	P-Panama	Voss (1967, 1971)
†*O. tetricus*	2.4	120,000–150,000	P	Australia	Joll (1976, 1983)
O. varunae	2.0*	-	P	I-India	Oommen (1971)
O. vitiensis	1.5–2.0	-	P	South Pacific	Pickford and Townsley (unpub.)
†*O. vulgaris*	1.5–2.7	100,000–500,000	P	Cosmopolitan	Boletzky (1969, 1971); Heldt (1948); Itami et al. (1963); Mangold (1983a); Mangold and Boletzky (1973); Naef (1928); Okutani et al. (1987); Pickford (1950); Rees (1950)
Euaxoctopus panamensis	1.4*	-	P	P-Panama	Voss (1971)
†*Hapalochlaena lunulata*	2.5–3.5	50+	P	IWP	Adam (1954); Overath and Boletzky (1974)
†*Robsonella australis*	2.0–2.8	1,000+	P	New Zealand	Benham (1942); Brough (1965); Pickford (1955)
R. fontanianus	1.3*–5.0	-	P	P-Peru to Chile	Thore (1959); Pickford (1955)
Scaeurgus patagiatus	2.0–2.5	-	P	P-Hawaii, Japan	Young et al. (1989)
†*S. unicirrhus*	2.0–2.5	-	P	A-Amphitropical, Mediterranean	Boletzky (1984); Mangold-Wirz (1963)
		INTERMEDIATE EGG SPECIES WITH EITHER SHORT DURATION PLANKTONIC OR BENTHIC HATCHLINGS			
Cistopus indicus	4.0–5.0*	-	P	Indo-Pacific	Pickford (1974)
Octopus chierchiae	3.8	10–35	B	P-Panama	Rodaniche (1984)
O. digueti	6.0–10.0	50–150	B	Gulf of California	Hochberg (1980, unpub.); Keferstein (1897); Perrier and Rochbrune (1894); Rochebrune (1896)
†*O. dofleini*	6.0–8.0	30,000–180,000	P	P-Japan to USA	Gabe (1975); Green (1973); Marliave (1981); Sasaki (1929); Yamashita (1974)

TABLE 6.—Continued.

Species	Length of egg capsule (mm)	Egg number	Habits of hatchlings	Geographical distribution	Reference
O. dollfusi	3.0–5.0	-	P	I-India	Sarvesan (1969)
†*O. fitchi*	4.0–6.0	150–300	P	Gulf of California	Hochberg (1980, unpub.)
O. fang-siao	5.0–8.0*	-	?	P-Japan	Saito (1934)
O. globosus	10.0	<100	?	P-Japan	Sasaki (1929)
O. joubini	6.0–10.0	25–300	B	A-Gulf of Mexico, Caribbean	Arocha (1983); Boletzky (1969); Boletzky and Boletzky (1969); Bradley (1974); Forsythe (1981a, 1981b, 1984a); Forsythe and Hanlon (1980); Hanlon (1983a, 1983b); Opresko and Thomas (1975); Thomas and Opresko (1973)
†*O. maorum*	4.0–6.0	7,000	P	New Zealand	Batham (1957); Stranks (1988b)
O. oshimai	6.0+	-	?	P-Japan	Sasaki (1929)
†*O. salutii*	5.2–6.0	2,000–4,000	P	Mediterranean	Boletzky (1977a); Mangold (1968); Mangold-Wirz (1963); Mangold-Wirz et al. (1976); Naef (1928)
O. zonatus	5.0–8.5	-	?	A-Caribbean to Colombia	Arocha (1983); Voss (1968)
Eledone caparti	8.9	2,800–5,100	?	A-Africa	Nesis and Nigmatullin (1978)
†*E. cirrhosa*	6.0–9.0	500–2,000	P	A, Mediterranean	Boyle (1983); Gravely (1909); Mangold et al. (1971); Morales (1958); Rees (1956); Russell (1922); Stephen (1944)
Hapalochlaena maculosa	6.0–9.0	100–200	B	P-Australia	Dew (1959); Reynolds (1983); Tranter and Augustine (1973)
Pteroctopus tetracirrhus	6.5–8.3	1,000–4,000	P	A-Amphitropical	Boletzky (1976, 1981a, 1988); Mangold (1965); Mangold-Wirz (1963, 1973)
			LARGE EGG SPECIES WITH BENTHIC YOUNG		
Octopus araneoides	13.0*	-	B	P-Japan	Taki (1964)
O. bimaculoides	12.0–17.0	200–750	B	P-California to Mexico	Forsythe et al. (1983); Hochberg and Fields (1980); MacGinitie and MacGinitie (1968); Pickford and McConnaughey (1949)
O. briareus	10.0–14.0	150–950	B	A-Caribbean	Boletzky (1969); Hanlon (1975, 1977, 9183a); Wolterding (1971)
O. californicus	12.0–15.0	50–100	B	P-California to Japan	Akimushkin (1965); Hochberg (unpub.)
O. conispadiceus	17.0–22.0 (28.0–30.0)	400–1,200	B	P-Japan	Ito (1983); Sasaki (1917b, 1929)
O. lobensis	9.0	-	B	A-Brazil	Palacio (1977)
O. maya	11.0–17.0	500–5,000	B	P-Mexico	Solis (1967); Van Heukelem (1976, 1977, 1983b)
O. microphthalmus	8.0–11.0	-	B	P-IWP	Pickford (1974); Pickford and Townsley (unpub.)
O. micropyrsus	8.0–10.0	25–45	B	P-California	Hochberg (unpub.); Hochberg and Fields (1980)
O. *minor* (= *variabilis*)	21.0–22.0	50–200	B	P-Japan	Okutani (1984); Yamamoto (1942)
O. ocellatus	9.5–13.0	600–1,000	B	P-Japan	Okutani et al. (1987); Sasaki (1929); Yamamoto (1941a, 1941b); Yamauchi and Takeda (1964)
O. pallidus	11.0–13.0	-	B	P-Australia	Stranks (1988a, 1988b)
O. superciliosus	9.0–11.0	300–350	B	P-Australia	MacPherson (1966); Stranks (1988b)
O. tehuelchus	10.0–15.0	80+	B	A-Brazil to Argentina	Castellanos (1970)
O. yendoi	17.0	-	B	P-Japan	Sasaki (1920, 1929)
Bathypolypus abruptus	12.0*	80	B	P-Japan	Sasaki (1929)

TABLE 6.—Continued.

Species	Length of egg capsule (mm)	Egg number	Habits of hatchlings	Geographical distribution	Reference
B. arcticus	9.0-14.0	20-80	B	A-Amphi-Atlantic	Macalaster (1976); O'Dor and Macalaster (1983)
B. faeroensis	18.0*	-	B	A-Denmark	Toll (1985)
B. sponsalis	8.0-15.0	7,000-8,000	B	Mediterranean	Mangold-Wirz (1963); Perez-Gandaras and Guerra (1978); Wirz (1954, 1955)
Bentheledone rotunda	16.0*	-	B	Australia to Antarctic	Hoyle (1886)
Benthoctopus januarii	14.0*	-	B	A-Brazil to Caribbean	Toll (1981)
B. leioderma	15.0	-	B	P-Boreal	Hochberg (unpub.)
B. magellanicus	21.0	-	B	A-Southern Argentina	Robson (1930)
B. piscatorum	12.0-21.0*	50+	B	A-Newfoundland	Aldrich and Lu (1968); Nixon (unpub.)
B. violaceus	13.0*	-	B	P-Japan	Taki (1964)
Benthoctopus sp.	25.0-28.0	50-75	B	P-Australia	Hochberg and Lu (unpub.)
Eledone massyae	10.0	-	B	A-Brazil	Palacio (1977)
E. moschata	12.0-16.0	100-500	B	Mediterranean	Boletzky (1975); Korschelt (1893); LoBianco (1909); Mangold (1983b)
Megaleledone senoi	17.0*	50+	B	Antarctic	Taki (1961)
Pareledone charcoti	7.0-13.0	-	B	Antarctic	Robson (1932a)
P. polymorpha	8.5-9.0*	-	B	Antarctic	Robson (1932a)
Vosseledone charrua	13.0*	40+	B	A-Brazil to Argentina	Palacio (1977, 1978
Graneledone sp.	35.0	50+	B	P-Peru	Hochberg (unpub.)

scattered through the literature. For comparison and completeness these have been included but the reader is cautioned that species without an asterisk need to be critically re-examined.

Planktonic stages can be identified to species with a high degree of confidence in cases where eggs and hatchlings are available from a known species of bottom-dwelling adult. Berry (1912) concluded that octopodid larval stages, in fact, were easier to identify than adults. Developmentally determined characters such as body shape, arm length formulae, and chromatophore and iridophore patterns can be used in species recognition.

Four characteristic arm-length patterns can be recognized in planktonic octopodid larvae (Figure 235). Most hatchlings have short, subequal arms. In the majority of species the arms elongate equally (see for example *Octopus rubescens, O. vulgaris, O. cyanea, O. dofleini,* and related genera *Scaeurgus, Berrya,* and *Eledone*). In the "*Macrotritopus*" complex, arms III are conspicuously elongated very shortly after hatching. In the Atlantic, this larval type has been identified as *O. defilippi.* Similar larvae have been found in plankton samples from the Pacific and Indian Ocean; however, details of morphology often differ indicating that a complex of species may be involved. In the Pacific, larval stages have been encountered in which arm pairs I and II are distinctly elongated. These stages are tentatively identified as belonging to the *O. macropus/ ornatus* complex. These larvae also have a characteristic elongate, cone-shape body. In the Pacific, off South America, planktonic larvae have been discovered in which arms II are conspicuously elongated. These larvae appear to belong to *Euaxoctopus panamensis* (Hochberg, unpublished). Thus, it appears that developmental patterns based on differences in arm lengths and body shapes may be distinct enough to warrant separation at the generic level.

The number and relative size of suckers at hatching can be used to separate species. In the eledonines, such as *Eledone,* suckers are added in a single row as the arms elongate. If added in two rows, the larvae belong to one of a number of species of octopodines. The number of suckers versus ML may be useful in differentiating species of planktonic larvae.

Species in which the arms are equal appear very similar to each other. However, chromatophore patterns can be used to provide a quick and relatively easy means of determining species visually. Founder chromatophores of several types are present in hatchlings and later planktonic stages. The founder chromatophores are the first chromatophores to appear in the development of the embryo and are the largest and deepest in the body. Founder chromatophores appear during late embryogenesis in a fixed sequence (see Fioroni, 1965; Packard, 1985). A few extrategumental chromatophores occur in the connective tissue at the base of the arms and covering the dorsal and ventral surfaces of the brain and eyes. A cluster of similar size, tegumental chromatophores are located in the skin covering the

dorsal surface of the viscera. However, the smaller and more numerous superficial tegumental chromatophores are often more conspicuous and easier to use for identification to species. The number and distribution of tegumental chromatophores in the skin covering the arms, funnel, mantle, and head are species specific. Tegumental chromatophores, especially in the region of the funnel, mantle, and arms, often persist in preserved material and provide the best visual cues to use in the identification of planktonic stages (Figures 255, 256).

The following definitions are used throughout for hatchling and larval chromatophore fields in octopod larvae. Similar fields are seen in other cephalopod larvae.

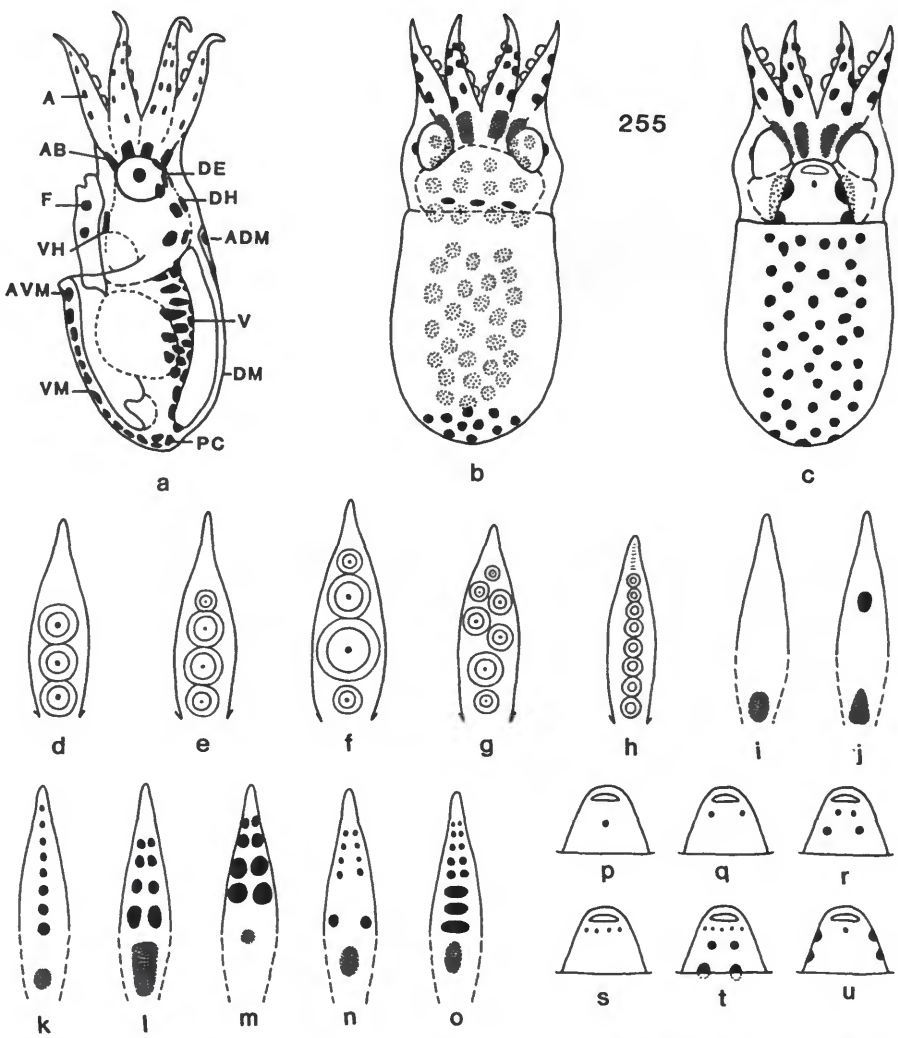
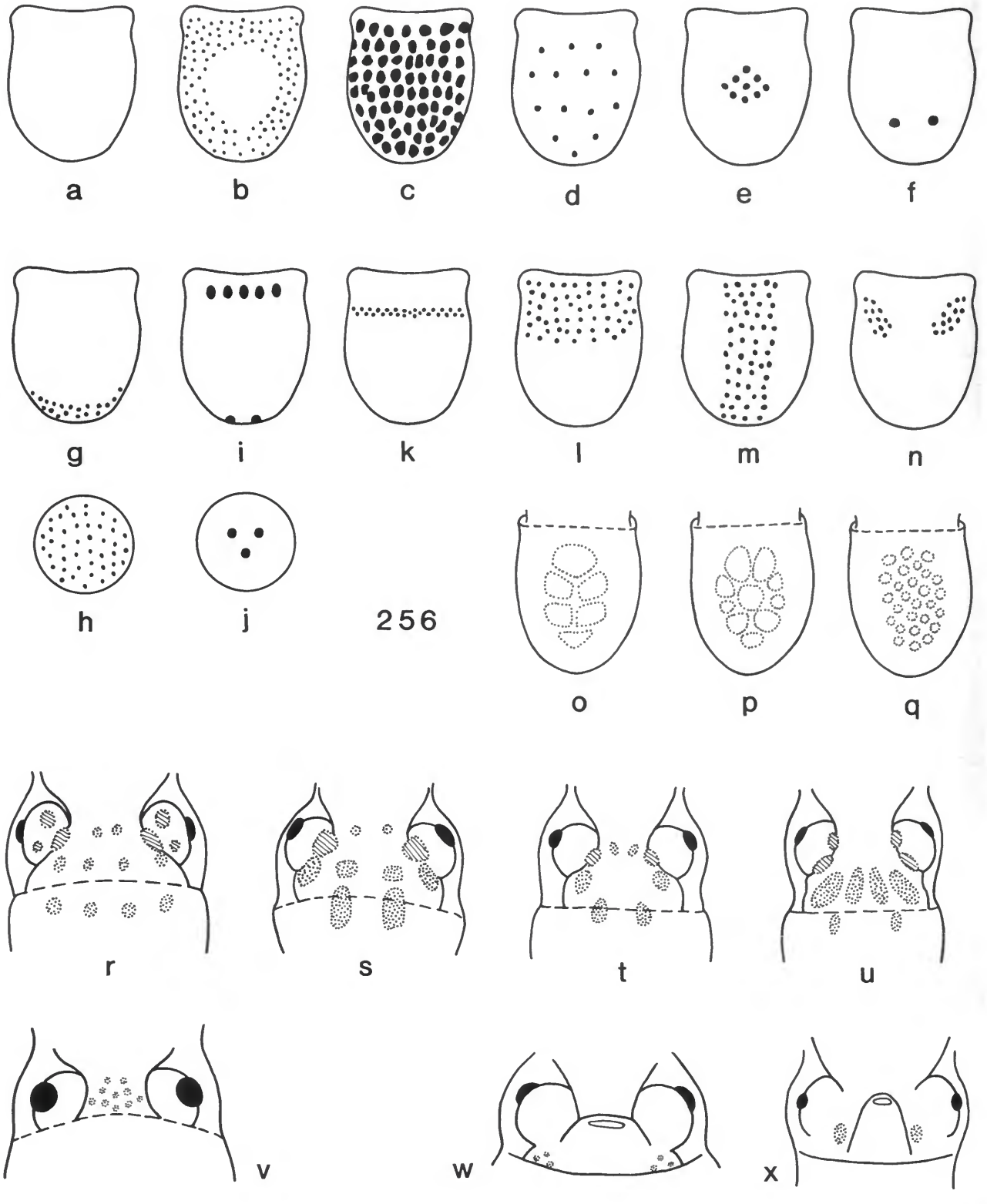


FIGURE 255.—Octopodidae, terminology for species-specific sucker and chromatophore patterns. Abbreviations for chromatophore fields: A = arm; AB* = arm base; ADM = anterior margin of dorsal mantle; AVM = anterior margin of ventral mantle; DE* = dorsal eye; DH* = dorsal head; DM = dorsal mantle; F = funnel; PC = posterior cap; V* = visceral; VH* = ventral head; VM = ventral mantle (* = extrategumental chromatophores). *a–c*, *Octopus* type E, distribution of chromatophore fields, 2.0 mm ML, Hawaiian Islands (redrawn from Young et al., 1989): *a*, left lateral view, optical section; *b*, dorsal view; *c*, ventral view (superficial or tegumental chromatophores are represented by stippled spots). *d–h*, arm suckers at the time of hatching, variations in number and size: *d–g*, *Octopus* spp. (from Young et al., 1989); *h*, *Eledone cirrhosa*. *i–o*, arm base (AB) and aboral arm (A) chromatophores in hatchlings, variations in number, size, and distribution: *i*, none; *j*, 1 spot (single chromatophore); *k*, 1 row; *l–n*, 2 rows; *o*, 1 + 2 rows. *p–u*, funnel chromatophores in hatchlings, variations in number, size, and distribution (not all patterns represented): *p*, 1; *q*, 2; *r*, 2 + 2; *s*, 4; *t*, 5 + 2 + 2; *u*, 1 + 2 + 2; (*h–u* original).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arm chromatophores = the small tegumental chromatophores located in the skin covering the aboral surface of each arm. Specific chromatophore patterns are counted from the base of the arm toward the tip (Figure 255*a,i–o*).

arm-base chromatophores = the single large extrategumental chromatophore located at the base of the brachial crown of each arm, deep in the head region in the connective tissue covering the muscles where the arms join the head (Figure 255*a,i–o*).

funnel chromatophores = the small tegumental chromatophores located in the skin covering the ventral surface of the funnel. Specific chromatophore patterns are counted from the lip of the funnel orifice toward the base of the funnel located under the anterior margin of the ventral mantle (Figure 255*a,p–u*).

mantle chromatophores = the small tegumental chromatophores located in the skin covering the dorsal, ventral, lateral, and posterior mantle. Specific patterns are counted across the mantle and/or posteriad from the anterior mantle margin (Figures 255*a*, 256*a–n*).

visceral chromatophores = the large tegumental chromatophores located deep in the mantle region in the integument (skin) covering the dorsal surface of the visceral mass (Figure 256*o–q*).

eye chromatophores = the large extrategumental chromatophores located in the head region in the connective tissue covering the dorsal and ventral surfaces of the eye (Figure 256*r–v*).

head chromatophores = the large extrategumental chromatophores located deep in the head region in the connective tissue covering the muscle of the dorsal and ventral head. Specific chromatophore patterns in the dorsal head are counted from the base of the arm crown toward the dorsal mantle margin (anterior to posterior). Additional, smaller tegumental chromatophores may be located in the skin covering the dorsal surface of the head (Figure 256*r–x*).

FIGURE 256 (oposite page).—Octopodidae, terminology for species specific chromatophore patterns: *a–n*, dorsal and/or ventral mantle chromatophores, variations in number, size, and distribution: *a*, entirely absent; *b*, absent in midregion, small chromatophores; *c*, densely covered, large chromatophores (9 across); *d*, sparsely covered, medium chromatophores (4 across); *e*, mid region patch; *f*, 2 spots; *g*, posterior margin; *h*, posterior cap, end view of figure above; *i*, anterior margin, simple band (5 across) plus posterior cap; *j*, posterior cap with 3 large chromatophores, end view of figure above; *k*, narrow, complex band (14–15 across, 2 rows); *l*, wide, complex band (8–9 across); *m*, wide, complex midline stripe (4–5 across, 12–13 in length); *n*, diagonal patchs. *o–q*, visceral chromatophores viewed through dorsal mantle, variations in number and size: *o*, few (6) large chromatophores; *p*, few (10) large chromatophores; *q*, many (20+) medium chromatophores. *r–v*, dorsal head (DH) and eye (DE) chromatophores, variations in number, size, and distribution: *r*, head 2 + 4 + 4 (large), eye 3; *s*, head 2 + 4 + 2, eye 1; *t*, head 2 + 2 + 2, eye 1; *u*, head + 4 + 2, eye 2; *v*, head, no pattern (scattered, small), eye 0. *w,x*, ventral head (VH) chromatophores, variations in number, size, and distribution: *w*, head, 3+/side (small), eye 0; *x*, head, 1/side (large), eye 0. (All original drawings.)

Species specific suites of dark chromatophores in several discrete fields (see above) are present at the time of hatching. These hatchling or stage I patterns are fixed and fully expressed at the time of hatching. Depending on the species, the number and distribution of chromatophores in the hatchling pattern may persist, without change, throughout the planktonic larval phase. In other species, the number of chromatophores may increase in all or only some of the chromatophore fields. The most consistent results in the identification of planktonic larval stages is achieved when the pattern at the time of hatching has been documented in detail for a given species.

Only a few taxa are described and figured here. In many cases additional material is needed to complete the description of the various growth stages in the plankton. In future studies it is essential to carefully figure and describe all aspects of the hatching stage in a standard format and to provide consistent details on later growth stages in order to enable critical comparison on a species by species basis. A worksheet useful in describing larval stages is provided here along with an illustrated guide to patterns observed (Figures 255, 256). Whenever possible vouchers of described and figured specimens should be deposited in a museum or archival institution.

This chapter represents the collective efforts of the 1985 CIAC octopod working group and the first author (Hochberg). It combines an extensive review of the literature with original observations. The goal was to assemble all published and unpublished records, descriptions, and figures of the eggs and planktonic larvae of the Octopodidae and to present this information in a standard format. As a *cautionary note*, it must be stressed that this is a preliminary study whose sole purpose is to summarize the current status of our knowledge. We have not diagnosed adult stages nor attempted to verify species or generic identifications—this will be done in the proceedings of the 1988 CIAC systematic workshop. Mistakes have undoubtedly been introduced and need to be corrected. Descriptions of larval stages need to be refined further and new figures prepared for most species. This document is simply a starting point. It should be used to help elucidate characteristic chromatophore and body shape patterns, to help unravel regional octopodid faunas and to further expand the diagnoses of species and genera. It should *not* be used as an identification manual without considerable reservation and without further critical study.

GENERAL REFERENCES.—Boletzky (1973, 1981b), Brocco, O'Clair, and Cloney (1974), Fioroni (1977, 1982), Forsythe and Hanlon (1985), Hanlon and Hixon (1983), Mangold-Wirz (1966, 1973), Mangold et al. (1988), Marliave (1981), Packard (1982, 1985), Querner (1927), Wells and Wells (1977), Young, Harman, and Hochberg (1989). Additional references are provided with each species description.

Octopus Lamarck, 1798

GENERIC CHARACTERS.—*Adults* (Figure 253*a*): Body small to large; mantle globose to ovoid, muscular; mantle

aperture wide; ocelli and other color patterns may be present; water pores absent; eyes normal size; arms short to long, subequal typically, 1.5-8.0 ×'s ML; suckers biserial, small to large, for a given species enlarged suckers may be present on either adult males or females or both; hectocotylus on right or left arm III; end organ small to large (1%-25% arm length), ligula size and shape varies; number of gill lamellae per outer demibranch varies; eggs small to large, hatchlings planktonic or demersal.

Young: See individual species accounts.

GEOGRAPHICAL DISTRIBUTION.—Cosmopolitan in shallow to moderate depths.

REMARKS.—Well over 200 nominal species have been named, of which less than 25% are described in sufficient detail to be consistently identified.

Octopus aegina Gray, 1849

SPECIES CHARACTERS.—*Young:* Hatchlings 2 mm ML (Figure 257*a*): arms short, subequal; number of suckers unknown; arms with 6 chromatophores in 2 rows; 1 large arm-base chromatophore per arm; funnel with 2 + 2 chromatophores; dorsal mantle pattern unknown; ventral mantle with simple band of 4-6 chromatophores on anterior margin and 10 chromatophores uniformly covering mid to posterior mantle; dorsal head and eye pattern unknown; ventral head without chromatophores; visceral chromatophore number and pattern unknown; presence of iridophores unknown.

GEOGRAPHICAL DISTRIBUTION.—Japan through Indo-west Pacific; Indian Ocean to Mozambique and Red Sea.

REFERENCES.—Eibl-Eibesfeldt and Scheer (1962).

Octopus alecto Berry, 1953

SPECIES CHARACTERS.—*Young:* Hatchling stage unknown.

Larvae 2.0 mm ML (Figure 257*b*): arms subequal with 6 suckers; arms with 12 chromatophores in 2 rows; 1 arm-base chromatophore per arm; funnel lip with 4 tiny chromatophores; dorsal mantle midregion without chromatophores, with 6 chromatophores in row on anterior margin, and 6-10 chromatophores visible in posterior region; ventral mantle uniformly covered with 60+ chromatophores (5-6 across); dorsal head with 20 chromatophores; eye chromatophore number unknown; ventral head with 2 chromatophores; visceral chromatophore number unknown; iridophores not visible.

Older stages in plankton not known.

GEOGRAPHICAL DISTRIBUTION.—Gulf of California, Mexico.

REFERENCES.—Berry (1953), CIAC Workshop (original observations), Hochberg (unpublished observations).

Octopus bimaculatus (Verrill, 1883)

SPECIES CHARACTERS.—*Young:* Hatchlings 2.6 mm ML (Figure 257*c*): arms short, subequal, about 1.0 mm long with 4 suckers; arms with 8 chromatophores in 1 + 2 row pattern; 1 arm-base chromatophore per arm; funnel with 4-5 tiny chromatophores on lip and 2 + 2 larger ones in mid region; dorsal mantle without chromatophores except for small cluster in posterior region; ventral mantle uniformly covered with over 40 chromatophores; dorsal head with 8 chromatophores (2 + 4 + 2 pattern); eye chromatophore number unknown; ventral head with 4 chromatophores per side; visceral chromatophore number unknown; iridophores not visible; ocelli not visible in larval stages.

Largest young recovered from plankton 6.0 mm ML (Figure 257*d,e*); arms develop second row of chromatophores at distal end; funnel chromatophore number and pattern remain same; chromatophore number and pattern on mantle and head remain same; gills with 10-11 lamellae per outer demibranch.

GEOGRAPHICAL DISTRIBUTION.—Eastern Pacific Ocean, California to Mexico, possibly to Panama.

REFERENCES.—Ambrose (1981), CIAC Workshop (original observations), Hochberg (unpublished observations).

Octopus burryi Voss, 1950

SPECIES CHARACTERS.—*Young:* Hatchlings about 1.5 mm ML (Figure 258*a-c*): arms short, subequal, with 4 suckers; arms with 8-10 chromatophores in 2 rows; funnel with 2 + 2 chromatophores; dorsal mantle clear; ventral mantle uniformly covered with 26-30 chromatophores (6 across); dorsal head with 10 large chromatophores between the eyes (2 + 4 + 4 pattern); 3 small chromatophores over each eye; ventral head with 2 chromatophores; dorsal surface digestive gland with 13 large visceral chromatophores; golden iridophores present around the eyes.

Largest young recovered from plankton 10.0 mm ML: arms with over 30 suckers in 2 rows; arms with over 30 chromatophores in 2 rows; funnel chromatophore number remains same; dorsal mantle uniformly covered with over 80 chromatophores; ventral mantle chromatophore number remains same; dorsal head chromatophore number increases to over 50; ventral head with 4 chromatophores; gills with 11 lamellae per outer demibranch.

GEOGRAPHICAL DISTRIBUTION.—Eastern Atlantic Ocean, Africa, Caribbean, and Gulf of Mexico.

REMARKS.—Forsythe and Hanlon (1985) provide figures that illustrate the embryonic development of chromatophore numbers and patterns. It is important to note that the above description indicates only the number and location of dark (brown) chromatophores, because the light or yellow ones are often not visible in preserved samples.

REFERENCES.—CIAC Workshop (original observations), Forsythe (1984b), Forsythe and Hanlon (1985), Voss (1951b).

Octopus cyanea Gray, 1849

SPECIES CHARACTERS (Australian larvae).—*Young:* Hatchlings 1.2-2.0 mm ML (Figure 259*a-c*): arms

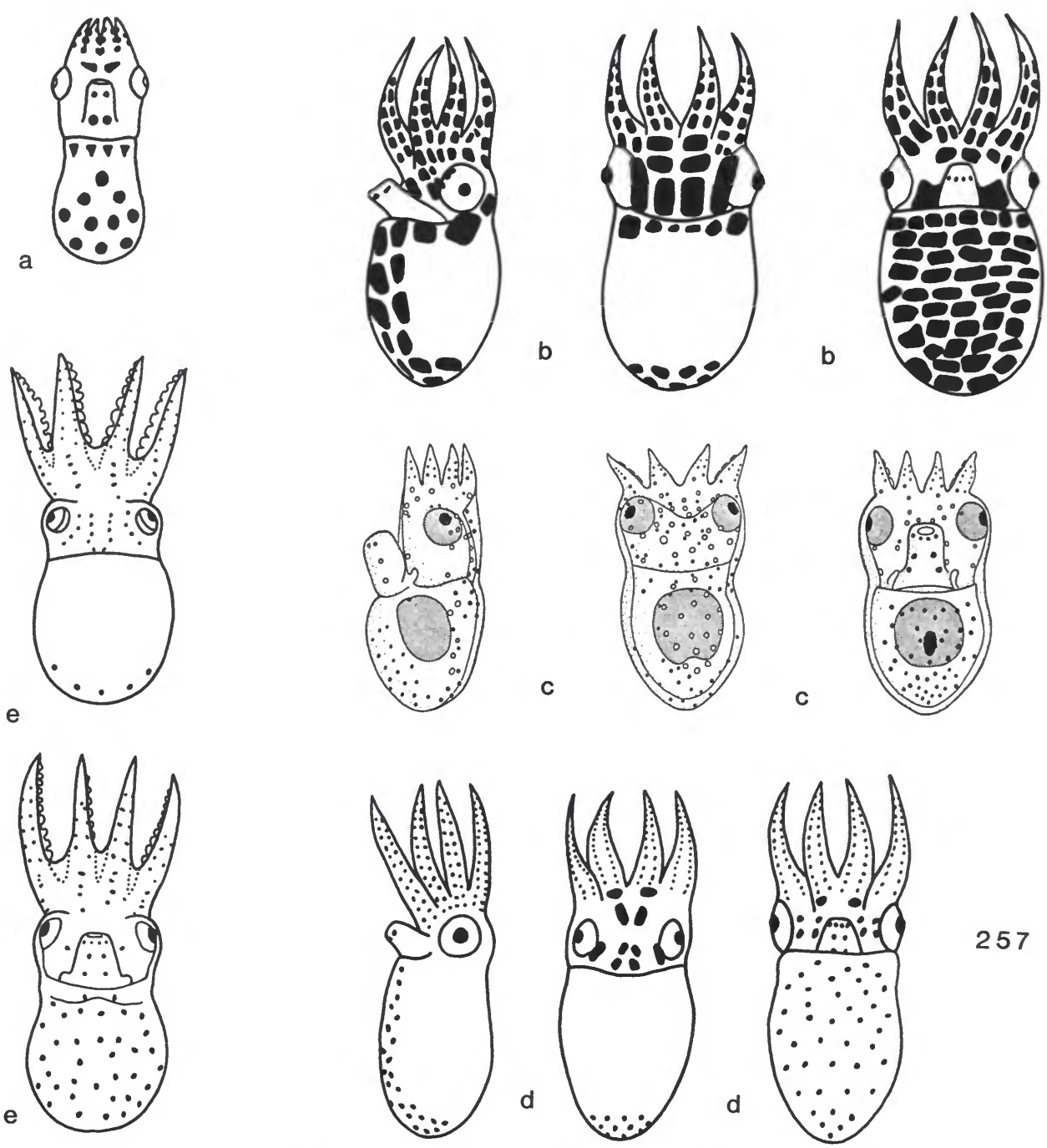

FIGURE 257.—Octopodidae: *a, Octopus aegina,* ventral view, hatchling emerging from egg, 1.8 mm ML, Nicobar Island (redrawn from Eibl-Eibesfeldt and Scheer, 1962); *b, Octopus alecto,* lateral, dorsal, and ventral views, young, 2 mm ML, Gulf of California (Forsythe original); *c–e, Octopus bimaculatus,* eastern North Pacific: *c,* lateral, dorsal, and ventral views, hatchling, 2.6 mm ML (from Ambrose, 1981); *d,* lateral, dorsal and ventral views, young, 6 mm ML (Hochberg original); *e,* dorsal and ventral views, newly settled young, 6 mm ML (Harman original).

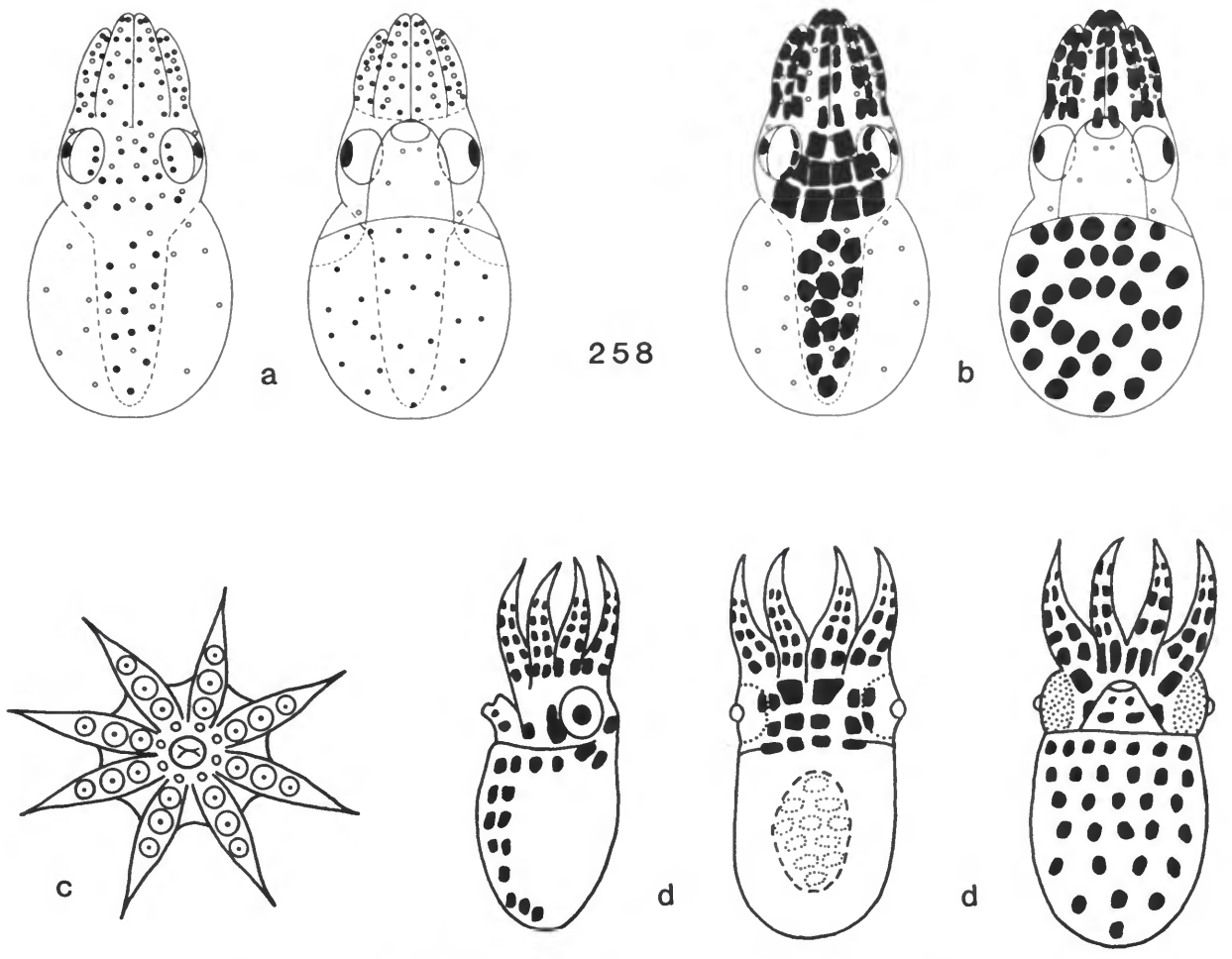

FIGURE 258.—Octopodidae, *Octopus burryi*, Gulf of Mexico: *a,b*, dorsal and ventral views, hatchling, 1.5 mm ML (from Forsythe and Hanlon, 1985): *a*, chromatophores relaxed (open circles = yellow; closed circles = brown); *b*, dark chromatophores expanded in live specimen. *c*, oral view, hatchling, 1.5 mm ML (Forsythe original). *d*, lateral, dorsal, and ventral views, young, 4.5 mm ML (Forsythe original).

short, subequal, with 3 suckers; arms with 2-3 chromatophores in 2 rows; funnel with 2 + 2 chromatophores; dorsal mantle mid region clear with 3–4 chromatophores in bar on anterior margin, and 4 chromatophores in posterior region; ventral mantle with over 20 widely spaced chromatophores; dorsal head with 10 chromatophores (2 + 4 + 4 pattern); eye chromatophore number unknown; ventral head with 4 large chromatophores; dorsal surface digestive gland with 6 large visceral chromatophores; iridophores not visible; ocelli not visible.

Older planktonic stages not known.

GEOGRAPHICAL DISTRIBUTION.—Australia.

REMARKS.—According to Stranks (pers. comm.) the common octopus species referred to as *O. cyanea* and studied off Sydney, Australia, by Dew, and LeSouef and Allan is not an ocellate species and hence is not *O. cyanea*. Although currently considered to represent an undescribed species, the description and figures are left here for convenience.

REFERENCES.—Dew (1959), LeSouef and Allan (1933, 1937), Stranks (1988b).

SPECIES CHARACTERS (Hawaiian larvae).—*Young:* Hatchlings 1.8 mm ML (Figure 259*d*): arms short, subequal with 3 suckers; arms with 4–5 chromatophores in 2 rows; 1 arm-base chromatophore per arm; funnel with 2 + 2 chromatophores; dorsal mantle mid region clear, with 3–4 chromatophores in bar on anterior margin and 4 chromatophores visible in posterior region; ventral mantle with 30–36 medium size chromatophores (5–6 across); dorsal head with 10 chromatophores (2 + 4 + 4 pattern); 1 large chromatophore per

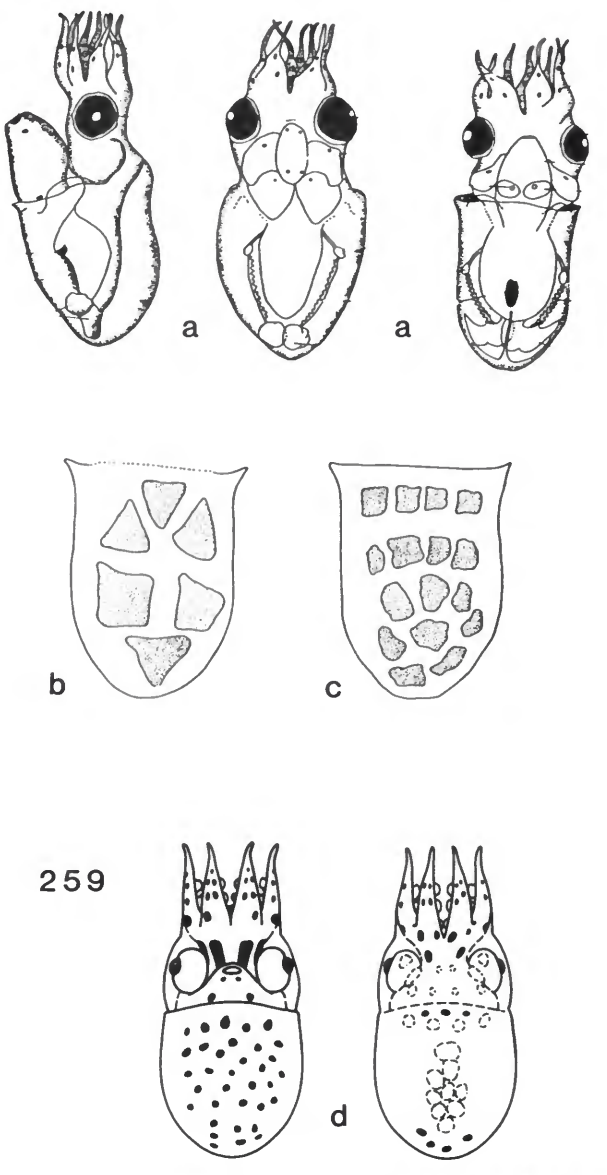

FIGURE 259.—Octopodidae, *Octopus "cyanea"*: *a*, lateral, dorsal, and ventral views, hatchling, 1.9 mm ML, western South Pacific (off Australia) (redrawn from Dew, 1959); *b*, dorsal mantle, supravisceral chromatophore pattern (from Dew, 1959); *c*, ventral mantle chromatophore pattern (from Dew, 1959); *d*, ventral and dorsal views, hatchling, 1.2 mm ML, Hawaiian waters (Young et al., 1989).

eye; ventral head with 4 chromatophores; dorsal surface of digestive gland with 9 visceral chromatophores; iridophores not visible; ocelli not visible.

GEOGRAPHICAL DISTRIBUTION.—Indo-West Pacific to Hawaii.

REFERENCES.—Van Heukelem (1973, 1983a), Wells and Wells (1970), Young, Harman, and Hochberg (1989).

**Octopus defilippi* Verany, 1851

SPECIES CHARACTERS.—*Young:* Hatchlings 1.3–1.5 mm ML (Figure 260*a*): arms subequal with 3 suckers; chromatophore patterns not known.

Post hatchlings 1.5–1.7 mm ML (Figure 260*b,c*): arms III elongated slightly with new sucker bud present; dorsal head chromatophores often visible, pattern unknown; additional chromatophore patterns unknown (Figure 260*a–g*).

Larvae 2.2–2.5 mm ML (Figure 260*d,e*): arms III conspicuously elongated with 11–15 suckers, other arms with 4–5 suckers; chromatophore patterns unknown.

Larvae 3.2 mm ML (Figure 260*f*): arms I, II, IV with 4 chromatophores and arms III with 14–16 chromatophores in 1 row; 1 chromatophore at base of each sucker; 1 large arm-base chromatophore per arm; funnel with 2 + 2 chromatophores; dorsal mantle without chromatophores in mid region, with 2 chromatophores in posterior region; ventral mantle with small cluster of 6–8 chromatophores in mid region; dorsal head with 8 chromatophores (2 + 4 + 2 pattern); 1 chromatophore over each eye; ventral head with 2 chromatophores; dorsal surface digestive gland with 11 large visceral chromatophores; gold iridophores around eyes, gills with 11 lamellae per demibranch.

Additional larvae 3.45–8.0 mm ML: figured (Figures 260*g*, 261*a–d*) but chromatophore patterns poorly defined.

Larvae 10.0 mm ML (Figure 261*e*): body elongate and tubular, bluntly rounded; arms I, II, IV with over 20 chromatophores and arms III with over 40 chromatophores in 1 row; 1 chromatophore at base of each sucker; funnel with 2 + 2 chromatophores; dorsal mantle without chromatophores in mid region, over 20 chromatophores in posterior region; ventral mantle chromatophore pattern and number unknown.

Largest young recovered from plankton 13.2 mm ML (Figure 261*f*): dorsal head with 2 + 2 + 4 pattern, other chromatophore patterns and numbers unknown.

GEOGRAPHICAL DISTRIBUTION.—Atlantic Ocean, Mediterranean and Caribbean seas.

REMARKS.—Larvae with elongate arms III also have been collected off South Africa and in the Indo-West Pacific from Hawaii to Australia. Differences in larval chromatophore patterns suggest that a species complex may be involved (compare with descriptions and figures of Hawaiian species, see below). In the past, planktonic octopod larvae with this arm configuration were assigned to the genus "*Macrotritopus*." Rees (1954a), Clarke (1969), Lu and Clarke (1975b), and others treated them as *Scaeurgus unicirrhus*. Issel (1925) was the first to correctly connect the planktonic stages with the adults and identify them as *O. defilippi*. This placement was later confirmed by Nesis and Nikitina (1981), Hanlon et al. (1980, 1985), and Boletzky (1984).

REFERENCES.—Boletzky (1977b, 1984), Clarke (1969), Degner (1925), Fioroni (1965), Hanlon, Forsythe, and Boletzky (1985), Hanlon, Hixon, and Forsythe (1980), Issel (1925), Joubin and Robson (1929), Lu and Clarke (1975b), Nesis and Nikitina (1981), Rees (1954a), Vecchione (unpublished observations), Voss (1964).

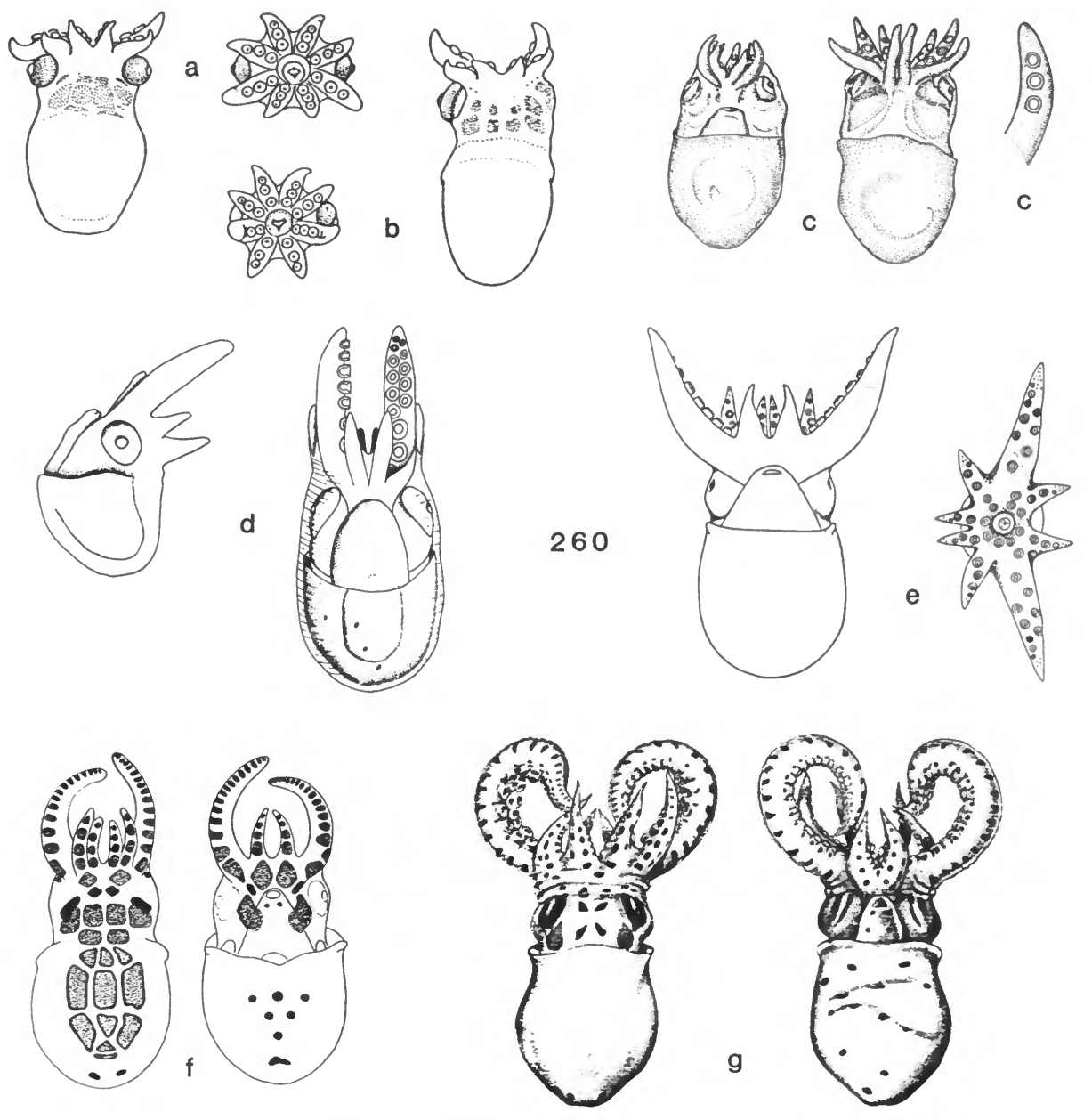

FIGURE 260.—Octopodidae, *Octopus defilippi: a,* dorsal and oral views, hatchling, 1.5 mm ML, eastern South Atlantic (off S. Africa) (from Hanlon et al., 1985); *b,* oral and dorsal views, young posthatchling, 1.7 mm ML, eastern South Atlantic (off S. Africa) (from Hanlon et al., 1985); *c,* ventral and dorsal views and oral surface of arm III, young posthatchling, 1.7 mm ML, Atlantic Ocean (from Nesis and Nikitina, 1981); *d,* lateral and ventral views; young, 2.2 mm ML, North Atlantic (from Clarke, 1969); *e,* ventral and oral views, young, 2.5 mm ML, North Atlantic (Vecchione original); *f,* dorsal and ventral views; young, 3.2 mm ML, Mediterranean (from Fioroni, 1965); *g,* dorsal and ventral views; young, 3.45 mm ML, English Channel (from Rees, 1954a).

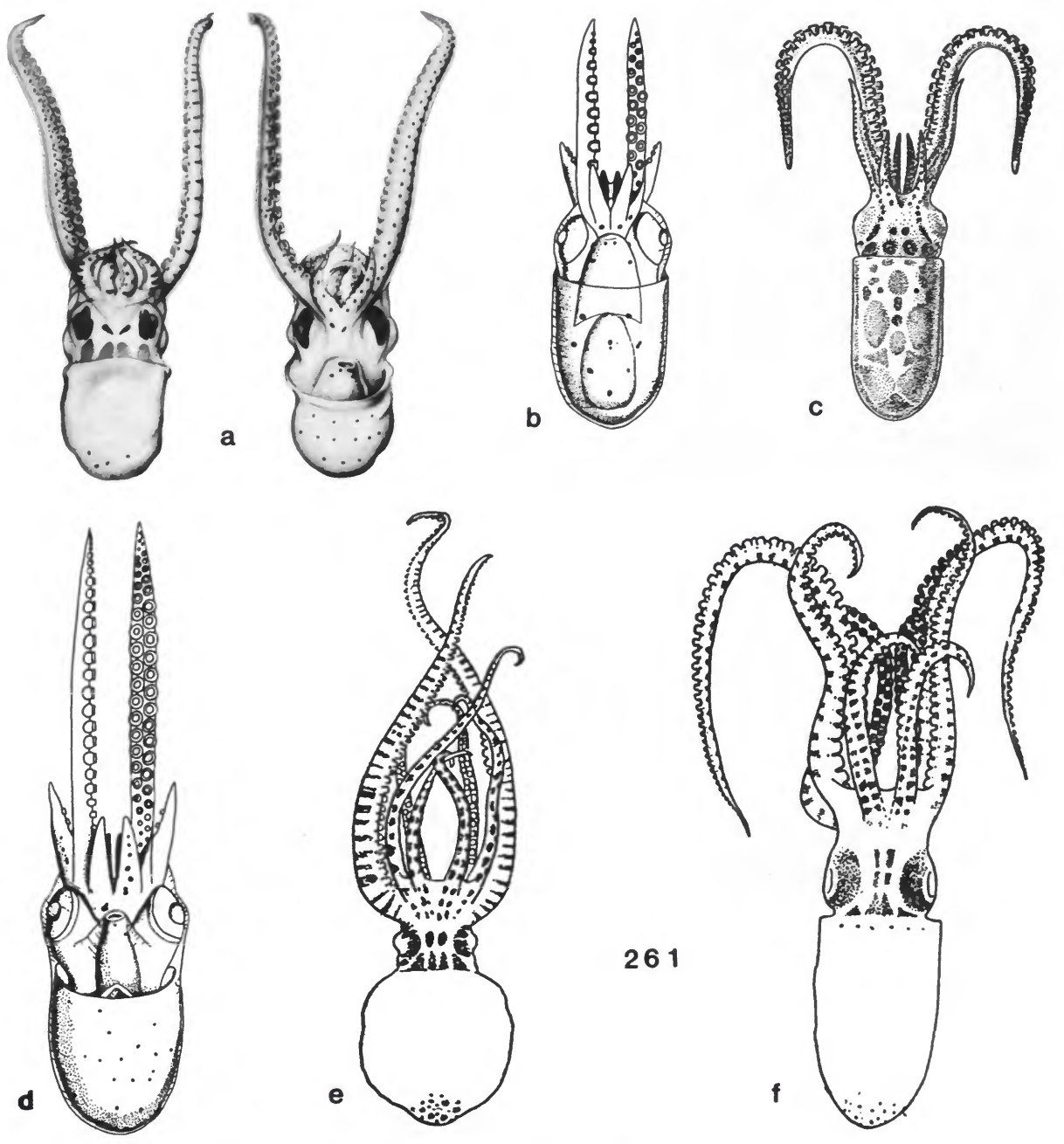

FIGURE 261.—Octopodidae, *Octopus defilippi* (cont.): *a*, dorsal and ventral views, young, 3.75 mm ML, English Channel (from Rees, 1954a); *b*, ventral view, young, 4.5 mm ML, North Atlantic (from Clarke, 1969); *c*, dorsal view, young, 6.6 mm ML, western North Atlantic (Vecchione original); *d*, ventral view, young, 8.0 mm ML, North Atlantic (from Clarke, 1969); *e*, dorsal view, young, 10.0 mm ML, eastern South Atlantic (off W. Africa) (redrawn from Robson, 1929a); *f*, dorsal view, young, 13.2 mm ML, North Atlantic (from Joubin and Robson, 1929).

SPECIES CHARACTERS (Hawaiian larvae) (This may not represent the same species but appears attributable to the same species complex).—*Young:* Hatchlings 1.6 mm ML (Figure 262*a*): arms short, subequal, with 3 suckers; arms without chromatophores; 1 large arm-base chromatophore on each ventral arm only; funnel with 2 chromatophores; dorsal and ventral mantle clear; dorsal head with 6 chromatophores (0 + 4 + 2 pattern); 1 large chromatophore per eye; ventral head without chromatophores; visceral chromatophore number unknown.

Larvae 3.1 mm ML (Figure 262*b*): arms III greatly elongated with 24 chromatophores in 2 rows, other arms subequal with 6–10 chromatophores in 2 rows; 1 large arm-base chromatophore per arm; funnel with 2 chromatophores; dorsal mantle clear; ventral mantle with 3 chromatophores in band in mid region; dorsal and ventral head pattern as above; eye pattern as above; visceral chromatophore pattern unknown.

Larvae 10.0 mm ML (Figure 262*c*): arms greatly elongated, 3>2>4>1; arm chromatophores in 2 distinct rows; funnel with 2 chromatophores; dorsal and ventral mantle without visible chromatophores; dorsal head and eye chromatophore patterns obscure; ventral head with 2 chromatophores; visceral chromatophore number unknown.

Largest stage in plankton 13.5 mm ML.

GEOGRAPHICAL DISTRIBUTION.—Hawaii.

REFERENCES.—Bower (1981), Newbert (1984, photographs), Young, Harman, and Hochberg (1989).

Octopus dofleini (Wulker, 1910)

SPECIES CHARACTERS.—*Young:* Hatchlings 3.0–3.5 mm ML (Figure 263*a–c*): arms subequal, 1.75 mm long, with 11–14 suckers; arms with 8–9 chromatophores in 1 row; funnel pattern complex, 4–8 chromatophores on lip plus 2 + 2 chromatophores in mid region; dorsal mantle clear in mid region, with band of 4–6 chromatophores on anterior margin

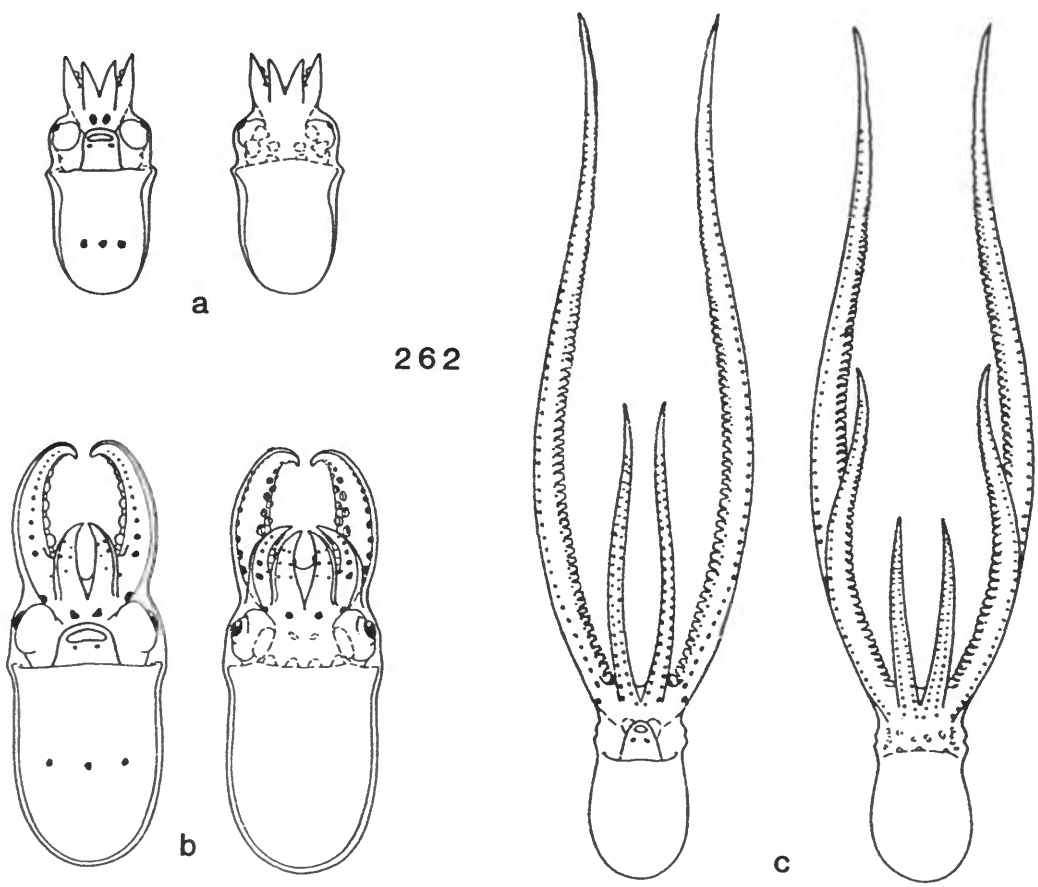

FIGURE 262.—Octopodidae, "*Octopus defilippi* complex," Hawaiian waters: *a*, ventral and dorsal views, hatchling, 1.3 mm ML (from Young et al., 1989); *b*, ventral and dorsal views, young, 2.7 mm ML (Young and Harman original); *c*, ventral and dorsal views, young, 9.0 mm ML (Young and Harman original).

and ring of about 40 chromatophores on side and in posterior region; ventral mantle devoid of chromatophores; posterior region with 10+ chromatophores visible ventrally; dorsal head with 8 chromatophores; eye chromatophore number unknown; ventral head with 2 chromatophores; visceral chromatophore number unknown; silver iridophores around eyes.

Larvae 5.0 mm ML: arms subequal; arms with 12-14 chromatophores in 1 row and 1 large chromatophore at base of

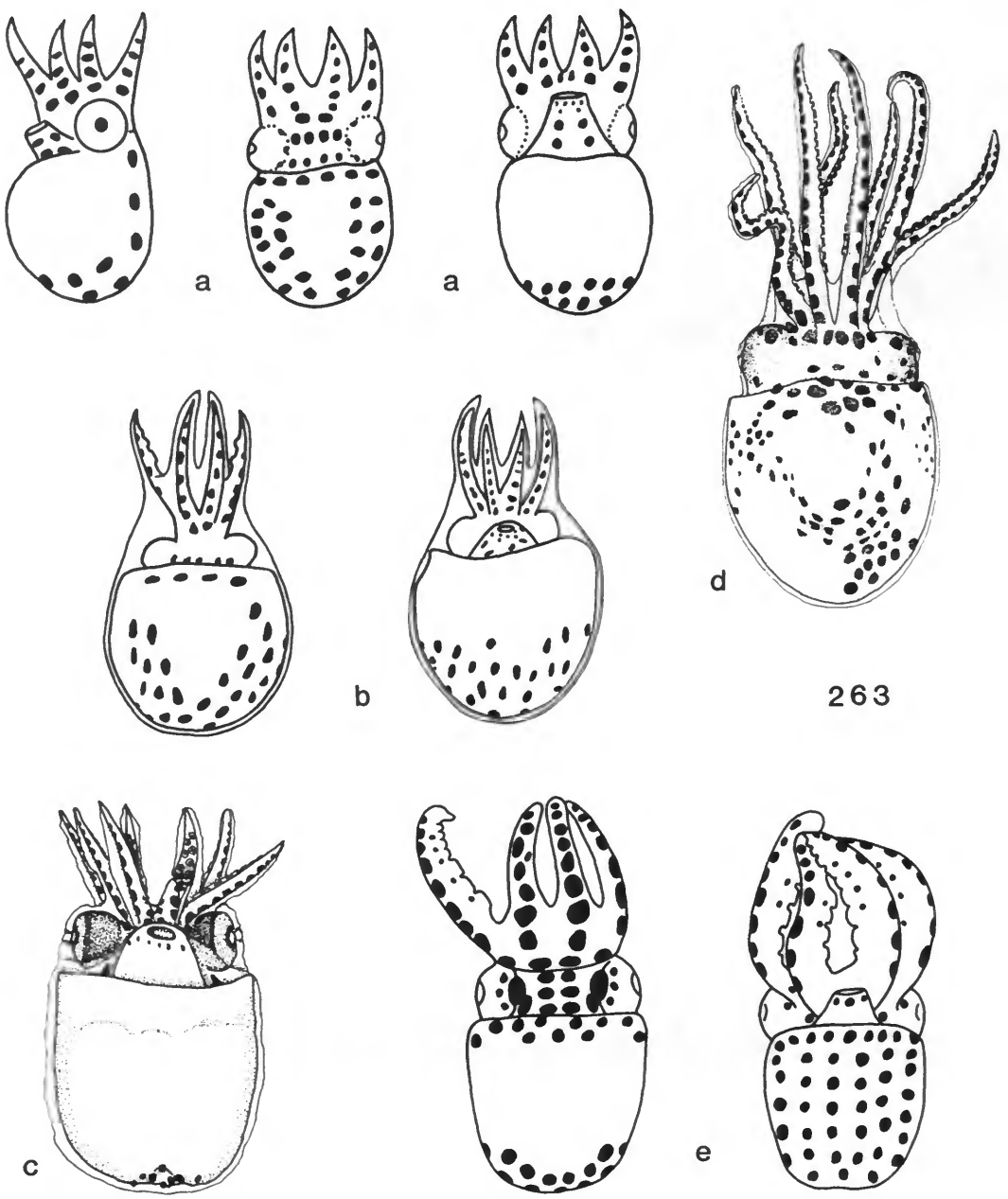

FIGURE 263.—Octopodidae: *a–d, Octopus dofleini: a,* lateral, dorsal, and ventral views, young posthatchling, 3.0 mm ML, eastern North Pacific (off Canada) (Lang original); *b,* dorsal and ventral views, young posthatchling, 3.0 mm ML, eastern North Pacific (off Canada) (redrawn from Green, 1973); *c,d,* young, northern North Pacific (Kubodera and Okutani, 1981): *c,* ventral view, 3.2 mm ML; *d,* dorsal view, 14.0 mm ML. *e, Octopus fitchi,* dorsal and ventral views, young posthatchling, 2.0 mm ML, Gulf of California (Hochberg original).

each arm; funnel pattern remains as above; dorsal mantle with 40–45 chromatophores (4–5 across), more densely covered to posterior; ventral mantle clear; dorsal head with 20–25 chromatophores, pattern obscure; 4 chromatophores over each eye; dorsal surface digestive gland with approximately 40 visceral chromatophores.

Largest young recovered from plankton 14.0 mm ML (Figure 263*d*): arms elongate, subequal, 18.2 mm long, with 40–50 suckers; arms with 15–20 chromatophores in 1 row; funnel chromatophore number and pattern as above; dorsal mantle with over 80 chromatophores in same pattern as hatchlings; ventral mantle chromatophore pattern and number unknown; dorsal and ventral head chromatophore patterns and numbers unknown; ventral head chromatophore pattern and number not known.

GEOGRAPHICAL DISTRIBUTION.—North Pacific Ocean, Aleutian arc, from Japan to California.

REFERENCES.—Fukida and Yamashita (1978), Gabe (1975), Green (1973), Hartwick (1983), Hochberg (unpublished observation), Kanamaru (1964), Kanamaru and Yamashita (1967), Kubodera and Okutani (1981), Marliave (1981), Mills (1983), Mottet (1975), Packard (1985), Yamashita (1974), Yamashita and Torisawa (1983).

Octopus fitchi Berry, 1953

SPECIES CHARACTERS.—*Young:* Hatchlings 2.0 mm ML (Figure 263*e*): arms subequal with 14–16 suckers; arms with 8 chromatophores in 1 row; arm base with 1 chromatophore per arm; 1 large chromatophore at base and on distal side of largest suckers in middle portion of each arm; funnel with 3 chromatophores on lip; dorsal mantle mid region clear, with band of 9–11 chromatophores on anterior margin and cap of 6–8 chromatophores in posterior region; ventral mantle densely covered with 42–44 chromatophores; dorsal head with 8 chromatophores (2 + 2 + 4 pattern); 1 large and 3 small

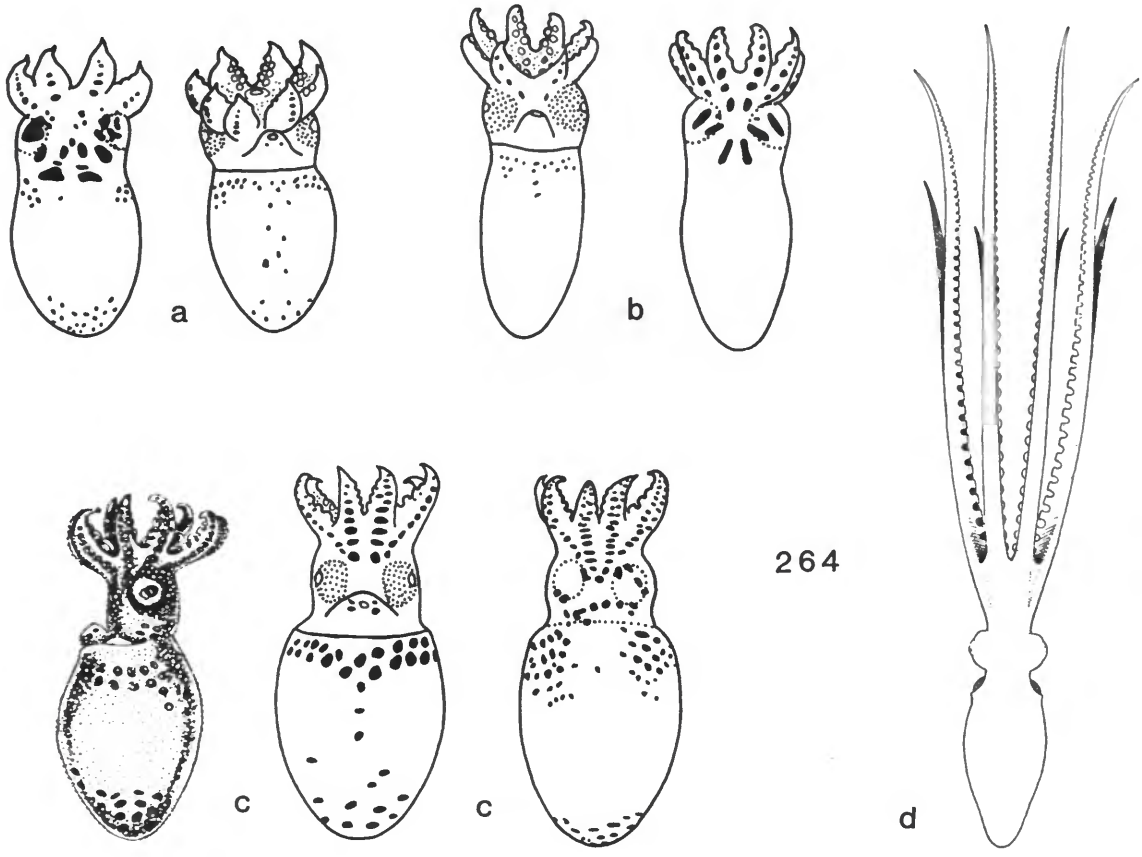

FIGURE 264.—Octopodidae, *Octopus macropus*, Mediterranean: *a*, ventral and dorsal views, young posthatchling, 2.4 mm ML (redrawn from Naef, 1923); *b*, ventral and dorsal views, young, 2.8 mm ML (redrawn from Naef, 1923); *c*, lateral, ventral, and dorsal views, young, 3.3 mm ML (lateral from Fioroni, 1978; others redrawn from Naef, 1928); *d*, dorsal view, recently settled juvenile, 22.0 mm ML (from Naef, 1923).

chromatophores over each eye; ventral head with 2 chromatophores and 1 small chromatophore over each eye; visceral chromatophore number unknown; iridophores not visible.

Larvae 2.5 mm ML: arms with 20–25 suckers; arms with 10–12 chromatophores in 1 row; remaining chromatophore numbers and patterns similar to hatchling; gills with 5–6 lamellae per outer demibranch.

GEOGRAPHICAL DISTRIBUTION.—Gulf of California, Mexico.

REFERENCES.—Berry (1953), Hochberg (1980, unpublished observations).

Octopus macropus Risso, 1826

SPECIES CHARACTERS.—*Young:* Hatchling stage unknown.

Larvae 2.4 mm ML (Figure 264*a*): arms short, subequal, with 7 suckers; arms with 4–6 chromatophores in 1 row; funnel with 4 chromatophores on lip; dorsal mantle with 12 chromatophores in 2 lateral diagonal patches in anterior region and 20+ chromatophores in posterior region; ventral mantle with 35+ chromatophores in distinct 2 row band on anterior margin and in 2 row midline stripe in mid region plus distinct posterior cluster with 20+ chromatophores; dorsal head with 14 chromatophores; eye chromatophore number unknown; ventral head chromatophore pattern and number not known; visceral chromatophore number unknown; iridophores not visible.

Larvae 3.3 mm ML (Figure 264*c*): body elongate, ovoid, tending toward conical; arms subequal with 10 suckers; arms with 16–20 chromatophores in 1 + 2 row pattern, second row starts distal to end of hatchling arm; funnel number remains same; dorsal mantle number increases to 30+ chromatophores, pattern remains same but diagonal patches increase in size; ventral mantle pattern the same, midline stripe may disappear; posterior cap number remains same; dorsal head increases to 18 chromatophores; ventral head chromatophore pattern and number unknown; visceral chromatophore number unknown.

Older stages in plankton: look like older stages of *O. ornatus;* body elongate, tapered, and distinctly conical; arm pairs I and II become distinctly elongate in later larval stages. Judging from youngest stages collected on the bottom (Figure 264*d*), larvae may remain in plankton to 15–20 mm ML.

GEOGRAPHICAL DISTRIBUTION.—Tropical Eastern and Western Atlantic Ocean and Mediterranean.

REFERENCES.—Adam (1945), Naef (1923, 1928), Rees (1955), Voss and Phillips (1957).

Octopus maorum Hutton, 1880

SPECIES CHARACTERS.—*Young:* Hatchlings 4.3–4.5 mm ML (Figure 265*a–c*): body elongate, mantle conical; arms subequal, 2.2 mm long, with 7–8 suckers; dorsal arms with 8–12 chromatophores in 1 + 2 row pattern, ventral arms with 6 chromatophores in 1 row; 1 arm-base chromatophore per arm; funnel with 2 chromatophores; dorsal mantle clear, with 2 chromatophores on anterior margin and 10–15 chromatophores visible in posterior region; ventral mantle with 5–8 chromatophores in band on anterior margin, with 4–6 chromatophores in cluster in mid region, and with 10–15 chromatophores visible

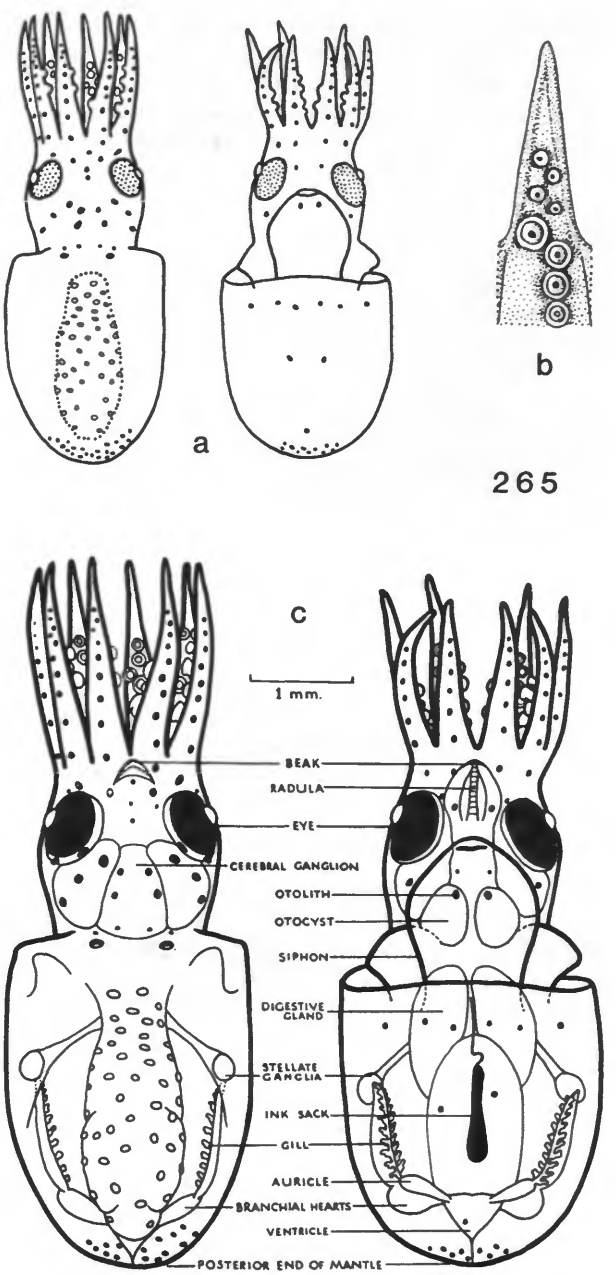

FIGURE 265.—Octopodidae, *Octopus maorum*, hatchling, 4.3 mm ML, western South Pacific (off New Zealand): *a*, dorsal and ventral views (redrawn from Batham, 1957); *b*, oral surface of arm (from Fioroni, 1978); *c*, dorsal and ventral optical sections (from Batham, 1957).

in posterior region; dorsal head with 9-12 chromatophores (probably 2 + 4 + 4 pattern); eye chromatophore number unknown; ventral head with 2 chromatophores; dorsal surface digestive gland with 40+ visceral chromatophores; iridophores not visible; gills with 10-11 lamellae per outer demibranch.

Other stages in plankton not known.

GEOGRAPHICAL DISTRIBUTION.—South Pacific Ocean, New Zealand, and Australia.

REMARKS.—Stranks (pers. comm.) recently confirmed the suggestion that *O. flindersi* from Australia is a junior synonym of *O. maorum* originally described from New Zealand.

REFERENCES.—Batham (1957), Brough (1965), CIAC Workshop (orignial observations).

Octopus ornatus Gould, 1852

SPECIES CHARACTERS.—*Young:* Hatchling 2.3 mm ML (Figure 266): arms with 9 chromatophores in 2 rows; funnel with 2 or 2 + 2 chromatophores; dorsal mantle clear; ventral mantle with 4-6 chromatophores in band on anterior margin; dorsal head with 10 chromatophores; ventral head clear; iridophores not visible.

GEOGRAPHICAL DISTRIBUTION.—In tropical waters, Indo-West Pacific Ocean, widely distributed from Hawaii to Australia. Specimens from the western Atlantic and Kenya may or may not represent this species.

REFERENCES.—Berry (1914), Voss (1981), Young, Harman, and Hochberg (1989).

Octopus rubescens Berry, 1953

SPECIES CHARACTERS.—*Young:* Hatchlings 1.7-2.0 mm ML (Figure 267*a*): body globose; arms short, subequal, with 4 suckers; arms with 6 chromatophores in 2 rows; 1 arm-base chromatophore per arm; funnel with 2 + 2 chromatophores; dorsal mantle clear in mid region, with simple band of 6 chromatophores on anterior margin and cap of 6-8 chromatophores in posterior region; ventral mantle densely covered with 30-40 chromatophores (6-7 across); dorsal head with 10 chromatophores (2 + 4 + 4 pattern); eye chromatophore number unknown; ventral head with 2 chromatophores; visceral chromatophore number unknown; gold iridophores around eyes.

Larvae 2.5 mm ML (Figure 267*b*): body ovoid; arms elongate with 6-8 chromatophores in 2 rows; funnel number and pattern as above; dorsal mantle clear with ring of 28-30 chromatophores, band on anterior margin not distinct at this stage; ventral mantle densely covered with 40-50 chromatophores (7-8 across); dorsal head number and pattern as above; 3 chromatophores per eye; ventral head with 2 chromatophores; visceral chromatophore number unknown.

Larvae 4.0 mm ML (Figure 267*c*): arms with 14-18 chromatophores in 2 rows; 1 chromatophore at base of each sucker; funnel number and pattern remain same; dorsal mantle chromatophore number increases to 30+, small clear region remains over digestive gland; ventral mantle number and pattern remain same; dorsal and ventral head chromatophore pattern and number remain same; gold iridophores around eyes.

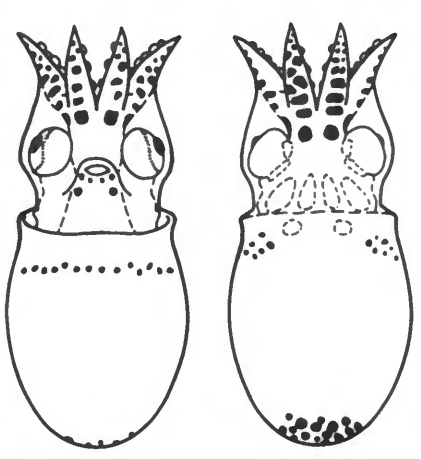

FIGURE 266.—Octopodidae, *Octopus ornatus*, Hawaiian waters, ventral and dorsal views, hatchling, 2.3 mm ML (from Young et al., 1989).

Larvae 10.0 mm ML (Figure 267*e*): arms with 32-34 chromatophores in 2 rows with 1 chromatophore at base of each sucker; funnel pattern and number remains same; dorsal and ventral mantle each densely covered with 80+ chromatophores, hatchling chromatophores remain large while new ones are smaller; dorsal head with 20+ chromatophores (pattern obscure); ventral head chromatophore number and pattern remain same; visceral chromatophore number unknown.

Oldest plankton stage: arms subequal, 48-54 mm long; body and arms densely covered with chromatophores, hatchling patterns obscured; gills with 12-13 lamellae per outer demibranch. Larvae typically settle out at approximately 10.0 mm ML. However, some may have extended life in plankton, up to 25.0 mm ML (Figure 267*d*).

GEOGRAPHICAL DISTRIBUTION.—Eastern Pacific Ocean, Alaska to Mexico and Gulf of California.

REFERENCES.—Berry (1911), Brocco, O'Clair, and Cloney (1974), Fisher (1923, 1925), Green (1973), Hochberg (unpublished observations), Mills (1983), Young (1972a).

Octopus salutii Verany, 1839

SPECIES CHARACTERS.—*Young:* Hatchling 3.5 mm ML (Figure 268*a*): arms short, subequal, 1.5 mm long with 4-5

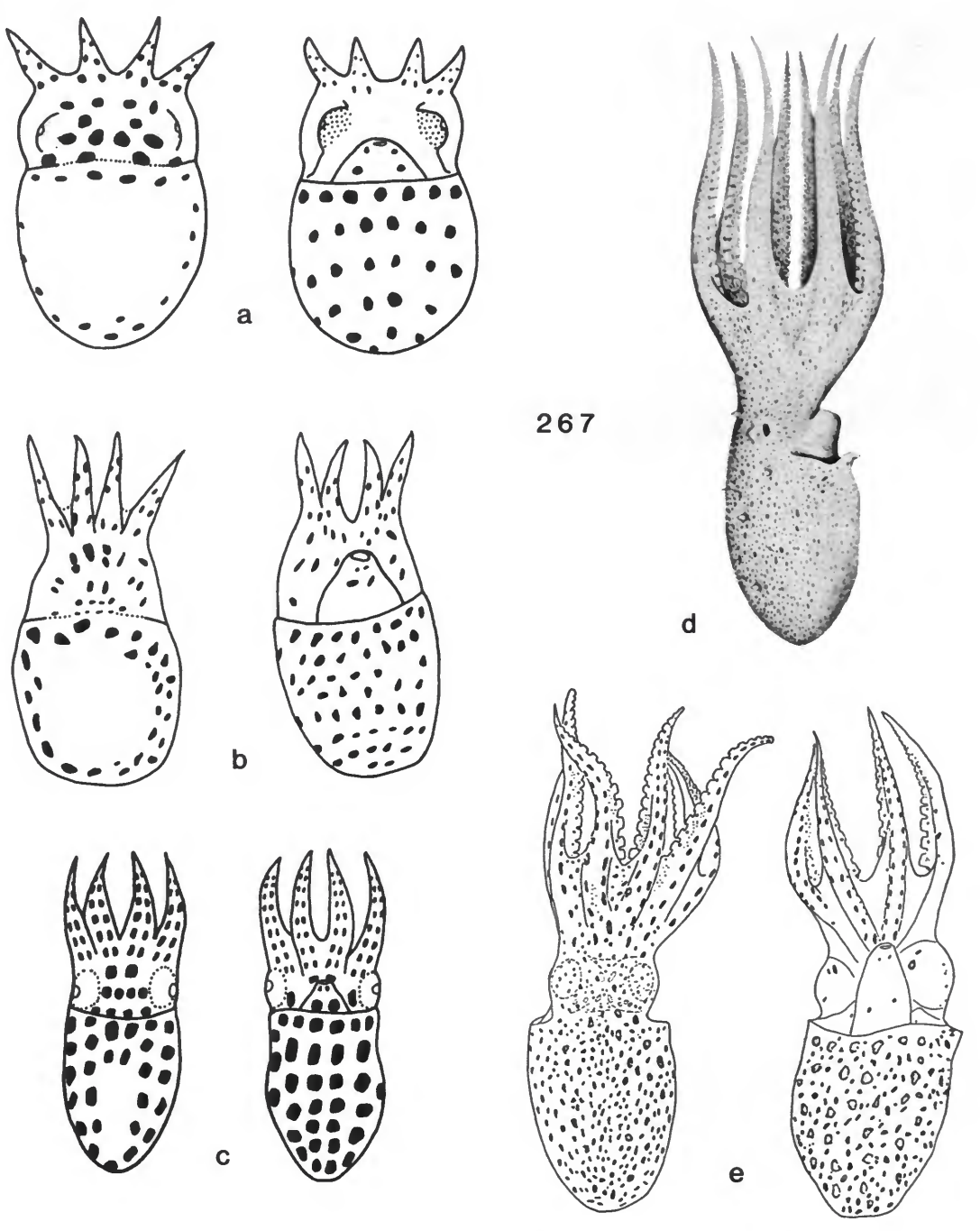

FIGURE 267.—Octopodidae, *Octopus rubescens*, eastern North Pacific: *a*, dorsal and ventral views, hatchling, 1.7 mm ML (Harman original); *b*, dorsal and ventral views, young, 2.5 mm ML (redrawn from Green, 1973); *c*, dorsal and ventral views, young, 4.0 mm ML, (Lang original); *d*, right lateral view, young, 16.0 mm ML (from Young, 1972a); *e*, dorsal and ventral views, recently settled benthic juvenile, 10.0 mm ML (from Green, 1973).

suckers; arms with chromatophores in 2 rows; chromatophores uniformly distributed over entire body surface; skin densely packed with Kolliker's organs, surface appears granular; gills with 7 lamellae per outer demibranch.

Older stages in plankton not known.

GEOGRAPHICAL DISTRIBUTION.—Mediterranean, Gulf of Biscay, eastern North Atlantic.

REFERENCES.—Mangold-Wirz, Boletzky, and Mesnil (1976).

Octopus tetricus Gould, 1852

SPECIES CHARACTERS.—*Young:* Hatchlings 1.3–1.6 mm ML (Figure 268*b*): arms short, subequal, 0.8 mm long, with 3 suckers; arms with 1–2 chromatophores in 1 row; 1 arm-base chromatophore per arm; funnel with 2 + 2 chromatophores; dorsal mantle clear in mid region, with 4 chromatophores in row on anterior margin; ventral mantle with 8–12 widely spaced chromatophores in mid to posterior region and 3 chromatophores in bar on anterior margin; dorsal head with 4 chromatophores (2 + 2 pattern); ventral head with 2 chromatophores; dorsal surface digestive gland with 7–8 large visceral chromatophores; gold iridophores around eyes.

Larvae 5.0 mm ML: arm chromatophores in 1 + 2 row pattern, second row added distal to end of hatchling arm; other chromatophore numbers and patterns remain same; dorsal head with 6 chromatophores (2 + 4 pattern); gold iridophores around eyes, especially ventral surface.

Largest young recovered from plankton 9.0 mm ML: arms subequal with 32 suckers; chromatophore numbers and patterns not described.

GEOGRAPHICAL DISTRIBUTION.—Eastern Indian Ocean, Australia.

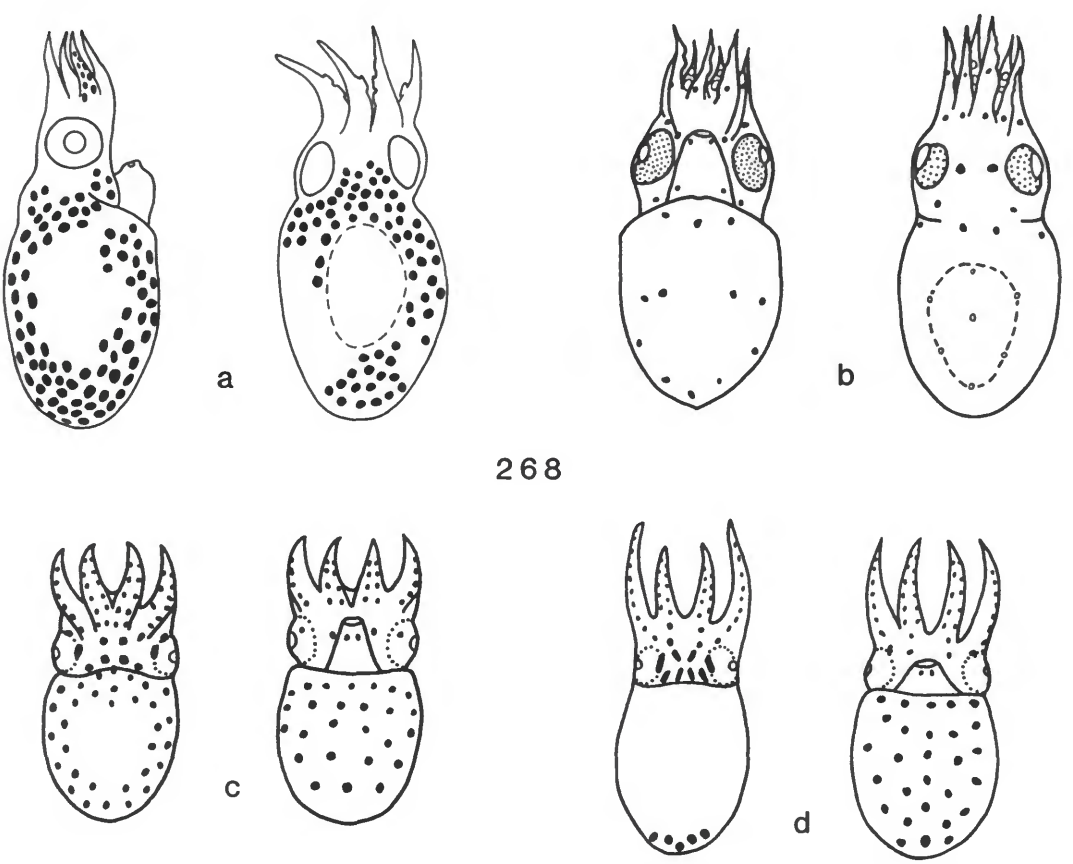

FIGURE 268.—Octopodidae: *a, Octopus salutii,* lateral and dorsal views, hatchling, 3.5 mm ML, Mediterranean (redrawn from unpublished Boletzky photographs of live animal; chromatophore pattern partially reconstructed); *b, Octopus tetricus,* dorsal and ventral views, hatchling, 1.6 mm ML, eastern Indian Ocean (off Australia) (redrawn from Joll, 1976) (open circles = supravisceral chromatophores); *c, Octopus veligero,* dorsal and ventral view, young, 5.0 mm ML, eastern North Pacific (off Baja California) (Hochberg original); *d, Octopus veligero,* dorsal and ventral views, young, 8.0 mm ML, eastern North Pacific (off Baja California) (Hochberg original).

REMARKS.—Allan (1945) identified as *O. tetricus* a 6.0 mm ML octopod larva from Australian waters but the figure and description are insufficient to confirm the identification. This specimen is figured in the section on unidentified octopodids at the end of this chapter.

REFERENCES.—Allan (1945), CIAC Workshop (original observations), Joll (1976, 1978, 1983).

Octopus veligero Berry, 1953

SPECIES CHARACTERS.—*Young* (Figure 268*c,d*): Hatchling stage unknown.

Smallest larvae known 4.0 mm ML: arms subequal with 9–12 suckers; arms with 12 chromatophores in 2 rows, with 1 chromatophore at base of each sucker; 1 arm-base chromatophore per arm; funnel with 2 ventral and 2 lateral chromatophores on lip; dorsal mantle mid region clear, surrounded by ring of 30+ chromatophores; ventral mantle uniformly covered with 30+ chromatophores; dorsal head with 6–10 chromatophores (2 + 4 pattern); 1 large chromatophore per eye; ventral head with 2 chromatophores; visceral chromatophore number unknown; gold iridophores extensively distributed around eyes, and on dorsal mantle, head, and arms.

Largest young recovered from plankton 10.0 mm ML: arms subequal with 40–50 suckers; arms with 30+ chromatophores in 2 rows; funnel chromatophore number and pattern remain same; dorsal mantle with 80+ chromatophores; ventral mantle uniformly covered with 80+ chromatophores; dorsal head with 60+ chromatophores; ventral head with 4–6 chromatophores; gills with 14 lamellae per outer demibranch.

GEOGRAPHICAL DISTRIBUTION.—Eastern Pacific Ocean, off Baja California, Mexico, and in Gulf of California.

REFERENCES.—CIAC Workshop (original observations), Hochberg (unpublished observations).

**Octopus vulgaris* Lamarck, 1798

SPECIES CHARACTERS (Atlantic and Mediterranean larvae).—*Young:* Hatchlings 1.5–2.0 mm ML (Figures 269*a–c;* 270*b,c*): mantle elongate, conical; arms subequal, 0.7 mm long with 3 suckers; arms with 2 chromatophores in 1 row; funnel with 2 + 2 chromatophores; dorsal mantle mid region clear, with 2 large chromatophores in posterior region; ventral mantle with 12–18 sparsely scattered large chromatophores; dorsal head with 8–10 chromatophores (2 + 4 + 4 pattern); 1 large chromatophore per eye; ventral head with 2 chromatophores; dorsal surface digestive gland with 6–7 large visceral chromatophores; blue-green iridophores around eyes.

Larvae 2.4 mm ML approximately 10 days old (Figure 269*d*): arms subequal, with 4–6 suckers; arms with 4 chromatophores in 1 row; funnel chromatophore number and pattern as above; dorsal mantle mid region clear with 2 large posterior spots of 1 chromatophore each; ventral mantle with 16–18 large chromatophores; dorsal and ventral head chromatophore numbers and patterns as above; visceral chromatophore number as above.

Largest young recovered from plankton 6.0 mm ML (Figure 269*h*): arms subequal, 7.0 mm long, with 20–26 suckers; arms with 20–28 chromatophores in 1 row proximally and 2 rows distally (1 + 2 pattern); funnel number and pattern same as in hatchlings; dorsal mantle mid region clear, ventral mantle covered with 25–30 chromatophores; dorsal and ventral head chromatophore number and pattern remain the same; gills with 9 lamellae per demibranch.

GEOGRAPHICAL DISTRIBUTION.—Cosmopolitan, eastern and western Atlantic Ocean, Mediterranean and Caribbean seas, Gulf of Mexico, western Pacific, Japan south.

REMARKS.—Larvae up to 10.0–11.0 mm ML may occur in plankton (see Rees, 1953). Itami et al. (1963) reported that Japanese larvae settled to the bottom 33–40 days after hatching. Newly settled animals ranged in size from 5.7–7.0 mm ML and had 21–27 suckers on each arm. Differences in sizes and chromatophore patterns of hatchlings between the eastern and western Atlantic Ocean suggest a species complex may be involved. Except for the paper by Itami et al. (1963), larvae from the western North Pacific Ocean have not been described in detail nor figured.

REFERENCES.—Boletzky (1969, 1973, 1974), Fioroni (1962, 1965, 1970, 1977, 1978), Inoue (1969), Itami et al. (1963), Mangold (1983a), Mangold and Boletzky (1973), Naef (1923, 1928), Nixon (1985), Packard (1985), Packard and Sanders (1969, 1971), Portmann (1933), Rees (1950, 1952, 1953), Rees and Lumby (1954), Vevers (1961).

Berrya Adam, 1939

GENERIC CHARACTERS.—*Adults:* Body medium size; mantle saccular, rounded; head and neck region as wide as mantle; skin soft, gelatinous, finely papillate; distinct lateral keel on mantle; conspicuous body color patterns and markings absent; mantle aperture very narrow; arms short, stout, rapidly tapered, subequal; suckers biserial, small, none enlarged; web very deep between all arms, 1/3–1/2 length of arm; wide brachial membrane on each arm; hectocotylus on right arm III; end organ small (3%–6% arm length), ligula conical, smooth, deeply excavated, calamus large; ink sac average size; funnel organ 2 V-shape pads; gills with 8–10 lamellae per outer demibranch. Monotypic.

Young: Unknown; on basis of egg size, larvae are presumed to be planktonic.

Eggs: Small (see Table 6).

GEOGRAPHICAL DISTRIBUTION.—Pacific Ocean, Japan to Hawaii, and Indo-Pacific to the Arabian Sea; deep water, 200–1000 m.

Berrya hoylei (Adam, 1939)

SPECIES CHARACTERS.—*Young:* Hatchlings and planktonic larvae are not known. The unidentified larva "Type G"

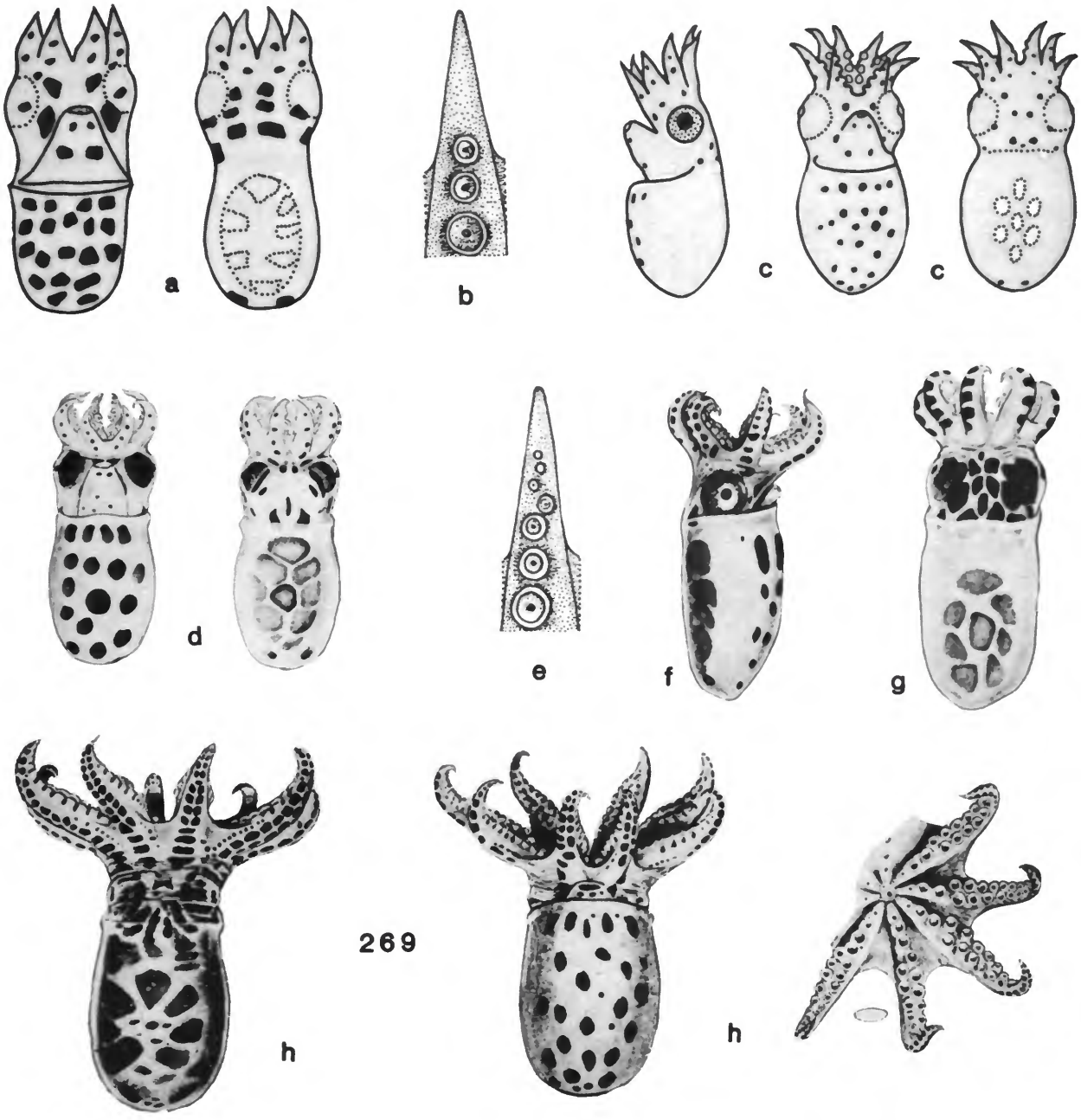

FIGURE 269.—Octopodidae, *Octopus vulgaris: a,* ventral and dorsal views, hatchling, 1.5 mm ML, Mediterranean (redrawn from Packard and Sanders, 1969); *b,* oral surface of arm, hatchling, (from Fioroni, 1978); *c,* lateral, ventral, and dorsal views, early posthatchling, 2.0 mm ML, Mediterranean (redrawn from Naef, 1923); *d,* ventral and dorsal views, young, 2.4 mm ML, English Channel (from Rees, 1950); *e,* oral surface of arm with developing sucker buds, young (from Fioroni, 1978); *f,* dorsal view, young, 3.15 mm ML, English Channel (from Rees, 1950); *g,* right lateral view, young, 3.75 mm ML, English Channel (from Rees, 1950); *h,* dorsal, ventral, and oral views, young, 6.0 mm ML, English Channel (from Rees, 1950).

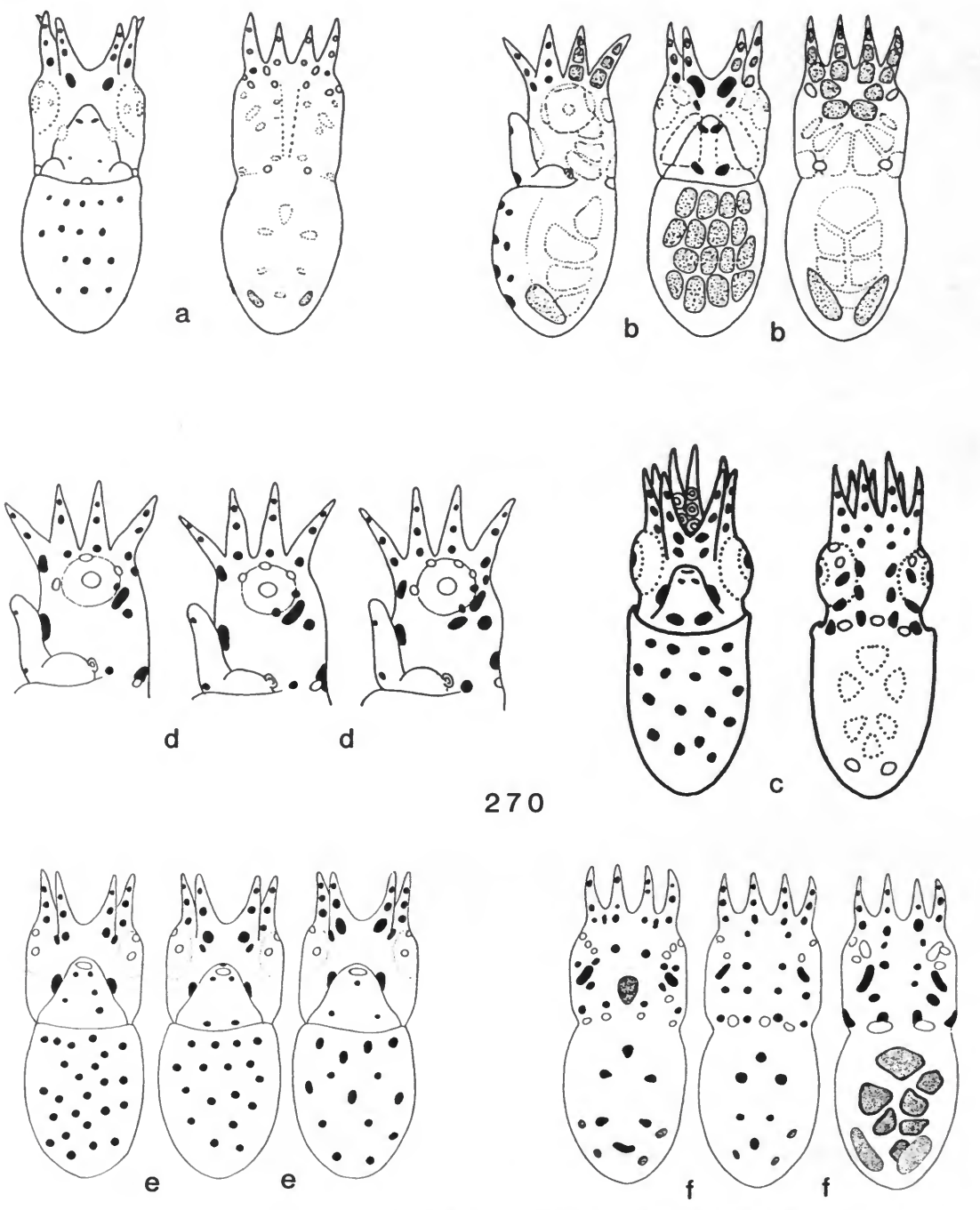

FIGURE 270.—Octopodidae, *Octopus vulgaris* (cont.), Mediterranean: *a*, ventral and dorsal views, hatchling, with chromatophores contracted (from Packard, 1985; modified from Fioroni, 1977) (dark spots = brown chromatophores; open circles = yellow chromatophores; dotted open circles = extrategumental chromatophores covering viscera and head); *b*, lateral, ventral, and dorsal views, hatchling, with chromatophores expanded (from Packard, 1985; modified from Fioroni, 1965); *c*, ventral and dorsal views, hatchling, 1.7 mm ML (from Fioroni, 1978); *d–f*, variations in chromatophore patterns, young (from Fioroni, 1965): *d*, left lateral view of head and arms; *e*, ventral views; *f*, dorsal views.

(Figure 277*a*) described and figured by Young et al. (1989) possibly represents this species.

GEOGRAPHICAL DISTRIBUTION.—See above for genus.

REFERENCES.—Adam (1939), Berry (1914), Taki (1963), Young, Harman, and Hochberg (1989).

Cistopus Hoyle, 1886

GENERIC CHARACTERS.—*Adults:* Body large; mantle elongate; head and neck region narrow, constricted; water pouches present as small pockets on web between each arm; distinct body color patterns and markings absent; arms long, slender, with attenuate tips, dorsal arms longest, arm formula I > II > III > IV; suckers biserial, none enlarged; hectocotylus on right arm III; end organ very small (3% arm length), ligula smooth and poorly developed; ink sac large, deeply embedded in digestive gland; gills with 10–11 lamellae per outer demibranch. Monotypic.

Young: Unknown; on basis of egg size larvae are presumed to be planktonic.

Eggs: Small (see Table 6).

GEOGRAPHICAL DISTRIBUTION.—Indo-Pacific.

Cistopus indicus (Orbigny, 1840)

SPECIES CHARACTERS.—*Young:* Unknown; larvae and juveniles identified as *O. teuthoides* may be related to this species.

GEOGRAPHICAL DISTRIBUTION.—As above for genus.

REFERENCES.—Pickford (1974), Voss and Williamson (1971).

Euaxoctopus Voss, 1971

GENERIC CHARACTERS.—*Adults:* Mantle small, ovoid, slender, bluntly pointed (to 40 mm ML); pair of distinct semicircular, dark patches on dorsal mantle; distinct constriction between mantle and head; head narrow; eyes small, protruding; web very shallow; water pores absent; arms very long, slender, arm formula II > III > I > IV; suckers biserial, small, none enlarged; hectocotylus on very short left or right arm III; end organ small to medium size (6%–9% arm length), ligula narrow, pointed, with strongly inrolled margins and fine transverse grooves; ink sac well developed, partially embedded in digestive gland; funnel organ VV; gills with 7–13 lamellae per outer demibranch.

Young: Typical of adults with extremely long arms II.

Eggs: Small (see Table 6).

GEOGRAPHICAL DISTRIBUTION.—Tropical western Atlantic (southern Caribbean to Surinam) and eastern Pacific (Gulf of Panama to Ecuador); in depths of 25–55 m.

REMARKS.—Of the two species described in this genus, namely *E. panamensis* (eastern Pacific) and *E. pillsburyae* (western Atlantic), egg size and planktonic stages are known only for the former species.

Euaxoctopus panamensis Voss, 1971

SPECIES CHARACTERS.—*Young:* Hatchling stage unknown.

Larvae 9.0 mm ML: body ovoid; arm pair II conspicuously elongated; chromatophore number and pattern unknown; gills with 11 lamellae per outer demibranch.

GEOGRAPHICAL DISTRIBUTION.—Gulf of Panama to Ecuador.

REFERENCES.—Hochberg (unpublished observations), Voss (1971).

Hapalochlaena Robson, 1929

GENERIC CHARACTERS.—*Adults* (Figure 253*c*): Body small, 40–50 mm ML, mantle elongate ovoid, pointed posteriorly; characteristic and conspicuous pattern of dark maculations and iridescent blue rings or bars on mantle and small blue rings on head, web, and arms; eyes small; arms short, subequal, 1–2.5 times ML; web deep; suckers biserial, small to minute, none enlarged; hectocotylus on right arm III; end organ small to medium size (5%–12% arm length), ligula smooth and flat, sides not inrolled; ink sac reservoir minute; water pores absent; gills with low number of lamellae (4–9 per outer demibranch).

Young: Cannot be distinguished from the young of *Octopus.*

Eggs: Small to medium (see Table 6); females of *H. maculosa* carry eggs in web while *H. lunulata* and *H. fasciata* attach them to the substrate (see Tranter and Augustine, 1973).

GEOGRAPHICAL DISTRIBUTION.—Genus restricted to Indo-West Pacific from Japan to Australia and Indian Ocean, occurs in tropical to temperate waters.

REMARKS.—A complex containing at least five species based on the patterns of iridescent rings and/or bars on the body and arms and on egg size (see Roper and Hochberg, 1988; Stranks, 1988b).

Hapalochlaena lunulata (Quoy and Gaimard, 1832)

SPECIES CHARACTERS.—*Young:* Hatchlings 2.3 mm ML: arms subequal, 1.1 mm long, with 10 suckers; arms with 2 rows of chromatophores; dorsal mantle clear, other chromatophore patterns and numbers not figured or described.

Older stages in plankton not known.

GEOGRAPHICAL DISTRIBUTION.—Indo-West Pacific Ocean and Indian Ocean.

REFERENCES.—Overath and Boletzky (1974), Roper and Hochberg (1988; for adult stages), Stranks (1988b).

Pteroctopus Fisher, 1882

GENERIC CHARACTERS.—*Adults:* Body medium size; mantle broadly ovoid; skin soft, gelatinous, covered with low, closely set tubercles; body color yellowish, distinct patterns and markings absent; mantle aperture very narrow; eyes normal size; arms medium length, subequal, 3 times ML; web very deep between all arms; suckers biserial, minute, embedded in swollen skin, none enlarged; hectocotylus on left arm III; end organ small to medium (5%–11% arm length), ligula conical, simple, with small calamus; ink sac average size, sits on top of digestive gland; water pores absent; funnel organ VV; gills with 9–10 lamella per outer demibranch. Monotypic.

Young: Unknown; on basis of egg size, larvae are presumed to be planktonic.

Eggs: Small (see Table 6).

GEOGRAPHICAL DISTRIBUTION.—Mediterranean and both coasts of North and South Atlantic Ocean; deep water 120–750 m.

Pteroctopus tetracirrhus (Chiaje, 1830)

SPECIES CHARACTERS.—*Young:* Neither hatchlings nor planktonic larvae have been figured or described.

GEOGRAPHICAL DISTRIBUTION.—As above for genus.

REFERENCES.—Boletzky (1976, 1981a, 1988), Lo Bianco (1909), Mangold (1965), Mangold-Wirz (1963, 1973), Morales (1973), Naef (1923).

Robsonella Adam, 1938

GENERIC CHARACTERS.—*Adults:* Body small to medium size, mantle globose, muscular; mantle aperture partly closed; ocelli, iridescent rings, maculations, or other distinct color patterns absent; eyes normal size; arms short, subequal, 2–3 times ML; web deep; suckers biserial, medium size, none enlarged; hectocotylus on right arm III; end organ medium size (8%–10% arm length), ligula stout, bulbous, with thick inrolled sides, groove deep and smooth; penis with long primary and small secondary diverticulum; ink sac present; water pores absent; gills with low number of lamellae (5–7 per outer demibranch). Cannot be distinguished from adult *Octopus*.

Young: Cannot be distinguished from young *Octopus*.

Eggs: Small (see Table 6).

GEOGRAPHICAL DISTRIBUTION.—Currently known from South America, Australia, and New Zealand.

REMARKS.—Pickford (1955) and others have argued that the genus was not valid because there were no specific characters that separate *Robsonella* from the genus *Octopus*. However, until a generic revision of the octopodines is completed by R. Toll we will leave the genus intact.

Traditionally, three species have been included in the genus. *R. fontaniana* (Orbigny, 1834) from South America is a valid species. *R. australis* (Hoyle, 1886) and *R. huttoni* Benham, 1943 originally described from New Zealand are synonymous (see Pickford, 1955). The problem is further complicated because *R. australis* occurs in Australia but is not synonymous with *O. australis* also found there. Stranks (pers. comm.) is working out the taxonomic status of the New Zealand and Australian species. Until a revision has been completed we will leave the genus and species intact for convenience of presentation.

**Robsonella australis* (Hoyle, 1885)

SPECIES CHARACTERS.—*Young:* Hatchlings 2.2–2.3 mm ML (Figure 271*a,b*): arms subequal, 1.0 mm long, with long tapered tips and with 4 suckers; arms with 3 chromatophores in 1 row; funnel with 1 chromatophore; dorsal mantle clear, with 2 chromatophores visible in region of posterior cap; ventral mantle with 4 chromatophores in band on anterior margin, with 6–8 chromatophores in band in mid region and with 1 chromatophore in posterior region; when viewed posteriorly cap has 3 chromatophores; dorsal head with 10 chromatophores (2 + 6 + 2 pattern); ventral head with 2 chromatophores; dorsal surface digestive gland with 13 visceral chromatophores; iridophores not visible.

Largest young recovered from plankton 5.0 mm ML: arms subequal with 14–18 suckers; arms with 7–9 chromatophores in 1 row; chromatophore number and pattern remain same as hatchling on funnel, dorsal, ventral, and posterior mantle, and dorsal head; ventral head with 4–6 chromatophores; iridophores not visible; gills with 6–8 lamellae per outer demibranch.

GEOGRAPHICAL DISTRIBUTION.—South Pacific Ocean; New Zealand.

REFERENCES.—Brough (1965), Fioroni (1978), CIAC Workshop (original observations).

Scaeurgus Troschel, 1857

GENERIC CHARACTERS.—*Adults* (Figure 253*b*): Mantle compact, globose, to 60 mm ML; body densely covered with rounded papillae, often fused into ridges; lateral mantle encircled by low keel or ridge; arm medium length, subequal, 3 times ML; web deep; suckers biserial, very small, none enlarged; hectocotylus on left arm III, arm markedly shorter than right arm III; end organ medium size (8%–11% arm length), ligula long, blunt, with swollen, infolded sides, groove deep with weakly developed transverse striae; penis with long diverticulum; funnel organ W-shape; ink sac present; water pores absent; gills with 11–14 lamellae per outer demibranch.

Young: Distinct body shape unlike *Octopus* larvae; mantle short and globose; head very wide; eyes large; funnel wide; arms short with filamentous tips; skin densely packed with opaque granules.

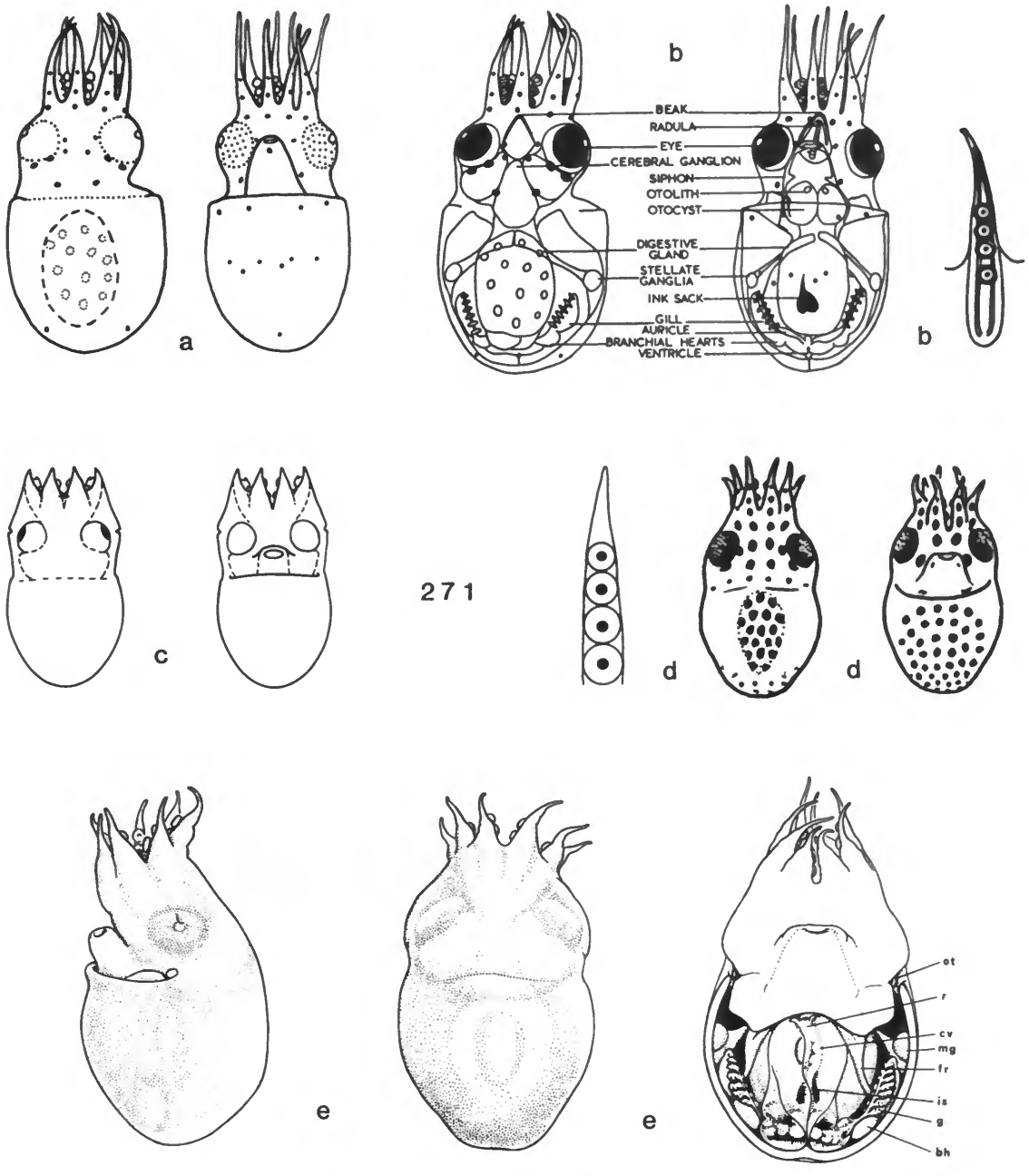

FIGURE 271.—Octopodidae: *a,b, Robsonella australis*, hatchling, 2.3 mm ML, western South Pacific (off New Zealand): *a*, dorsal and ventral views showing chromatophore pattern (redrawn from Brough, 1965); *b*, dorsal and ventral optical sections and oral surface of arm (from Brough, 1965) (open circles = supravisceral chromatophores). *c*, *Scaeurgus patagiatus*, dorsal and ventral views, hatchling, 1.6 mm ML, Hawaiian waters (Young et al., 1989). *d,e*, *Scaeurgus unicirrhus*, live hatchling, Mediterranean (from Boletzky, 1984): *d*, oral view of arm with suckers, dorsal and ventral views, 2.0 mm ML; *e*, lateral, dorsal, and ventral views, latter with mantle removed, 2.5 mm ML (bh = branchial heart; cv = cephalic vein; fr = funnel retractor; g = gill; is = ink sac; mg = mantle ganglion; ot = olfactory tubercle; r = rectum).

Eggs: Small (see Table 6).

GEOGRAPHICAL DISTRIBUTION.—Genus is circumglobal, in scattered tropical and warm temperate localities.

REMARKS.—Two species have been described. Recent comparative studies on larvae (Young et al., 1989) and adult morphology (Toll, 1988) indicate that Berry's (1913) species *S. patagiatus* (Figure 270*d*) is distinct from *S. unicirrhus* (Figure 270*e*) and not a synonym as originally proposed by Robson (1929b) and Voss (1951a).

Scaeurgus patagiatus Berry, 1913

SPECIES CHARACTERS.—*Young:* Hatchlings 1.5 mm ML (Figure 271*c*): body globose; arms very short, subequal, with 4 suckers; arms I and II with 1 chromatophore, arms III with 2 chromatophores in 1 row, arms IV with 3 chromatophores in 1 row; dorsal and ventral mantle clear; dorsal head with 4 chromatophores (2 + 2 pattern); 1 chromatophore per eye; ventral head chromatophore number unknown; dorsal surface of digestive gland with 8–10 visceral chromatophores; iridophores not visible; skin densely covered with Koelliker's bristles.

Older stages in plankton not known.

GEOGRAPHICAL DISTRIBUTION.—North Pacific Ocean, Indo-West Pacific (Japan to Hawaii).

REMARKS.—The unidentified larva "Type F" described and figured by Young et al. (1989) is assigned to this species.

REFERENCES.—Berry (1913), Young, Harman, and Hochberg (1989).

**Scaeurgus unicirrhus* Orbigny, 1840

SPECIES CHARACTERS.—*Young:* Hatchlings 2.0 mm ML (Figure 271*d*): body squat, globose; arms short, subequal, with 4 suckers; arms with 3–4 chromatophores in 1 row; 1 arm base chromatophore per arm; funnel with 2 + 2 chromatophores; dorsal mantle clear, with about 10 chromatophores in posterior region; ventral mantle with large cluster of 35–40 chromatophores in mid to posterior region; dorsal head with 14 chromatophores (4 + 4 pattern); eye chromatophores unknown; ventral head with 2 large chromatopores; dorsal surface digestive gland with 20 visceral chromatophores; iridophores not visible; skin appears densely packed with calcareous granules.

Larvae 2.5 mm ML (Figure 271*e*): similar to hatchlings; arms with 4 suckers; chromatophore patterns faded and unknown; skin densely packed with Koelliker's bristles; gills with 7 lamellae per outer demibranch.

Older planktonic stages unknown.

GEOGRAPHICAL DISTRIBUTION.—Mediterranean, eastern and western Atlantic Ocean.

REFERENCES.—Boletzky (1977b, 1984), Naef (1928), Voss (1951a).

Eledone Leach, 1817

GENERIC CHARACTERS.—*Adults* (Figure 253*d*): Mantle ovoid, broad, to 400 mm ML; body covered with fine, closely set warts; lateral mantle encircled by low keel or ridge; arms short, stout, subequal, 2–3 times ML; suckers uniserial, medium size, may be enlarged in males; suckers near tips of arms of males modified into flattened platelets or minute, fleshy papillae; hectocotylus on right arm III, arm shorter then left arm III; end organ small (3%–4% arm length), indistinct, not differentiated into ligula and calamus; funnel organ \/\-/- *or* W-shape; ink sac present; cephalic water pore absent; gills with 8–12 lamellae per outer demibranch.

Young: Similar in size and shape to *Octopus* larvae; entire body covered with large chromatophores; as suckers are added they never form 2 rows.

Eggs: Small to large (see Table 6).

GEOGRAPHICAL DISTRIBUTION.—North and South Atlantic, Mediterranean, Indo-West Pacific in warm to cool temperate waters.

**Eledone cirrhosa* (Lamarck, 1798)

SPECIES CHARACTERS.—*Young:* Prehatchlings (Figure 272*a*).

Hatchlings 3.7–4.0 mm ML (Figure 272*b*): body globose to slightly elongate and conical; arms subequal, 2.5–2.8 mm long, with 8 suckers in 1 row; arms with 8–11 chromatophores in 1 row; funnel with 2 chromatophores, located laterally on lip; dorsal mantle densely covered with 50+ chromatophores, may have clear area over digestive gland; ventral mantle densely covered with 50+ chromatophores; dorsal head with 6+ chromatophores (2 + 4 pattern); 8+ chromatophores per eye; ventral head chromatophore number and pattern unknown; dorsal surface of digestive gland with 13 visceral chromatophores; silver iridophores around eyes.

Largest young recovered from plankton 12.0 mm ML: arms subequal, 16.0 mm long, with over 28 suckers in 1 row; chromatophore number and patterns appear to be same as hatchlings.

GEOGRAPHICAL DISTRIBUTION.—Mediterranean and eastern North Atlantic.

REMARKS.—Specific details of the development of chromatophores and the number and patterns at the time of hatching should be reinvestigated for detailed comparisons with the patterns of *Octopus* larvae.

REFERENCES.—Boletzky (1977a), Boyle (1983), Boyle and Knobloch (1983), Fioroni (1965), Fuchs (1973), Joubin (1888), Mangold-Wirz (1963), Mangold, Boletzky, and Froesch (1971), Moriyasu (1981, 1983), Portmann (1937), Rees (1956), Sacarrao (1943), Stephen (1944).

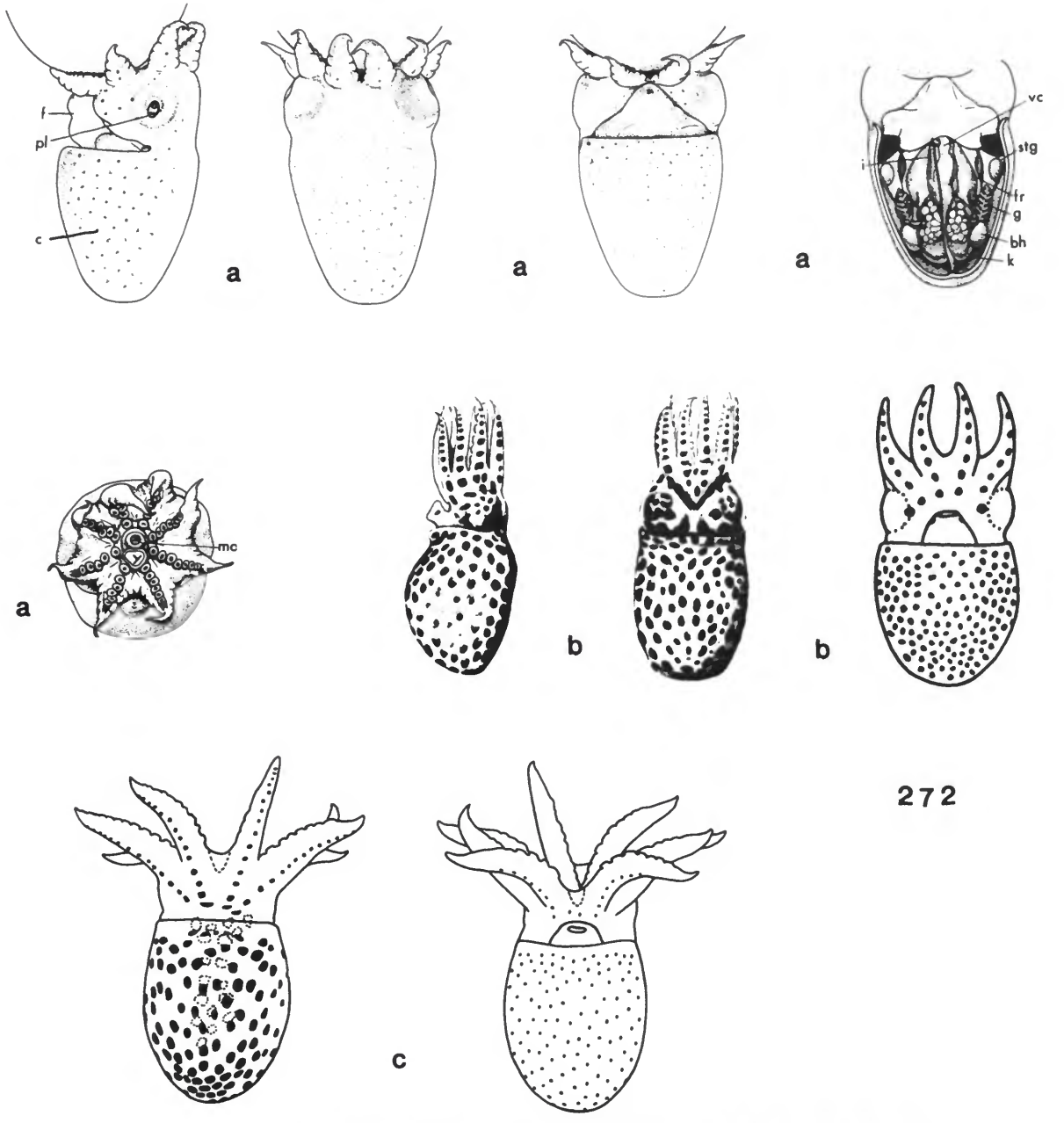

FIGURE 272.—Octopodidae, *Eledone: a,b, Eledone cirrhosa: a*, lateral, dorsal, ventral, mantle cavity and oral views, prehatchling (Stage XIX), 3.2 mm ML, Mediterranean (from Mangold et al., 1971) (bh = branchial heart; c = chromatophore; f = funnel; fr = funnel retractor; g = gill; i = intestine; k = renal sac; mo = mouth; pl = primary lid; stg = stellate ganglion; vc = vena cava; y = yolk); *b*, lateral, dorsal, and ventral views, hatchling, 3.8 mm ML, English Channel (from Rees, 1956; ventral view, Hochberg original). *c, Eledone nigra*, dorsal and ventral views, young, 6.9 mm ML, eastern South Atlantic (off S. Africa) (redrawn from photograph in Rees, 1954b) (stippled circles = chromatophores on head and dorsal viscera).

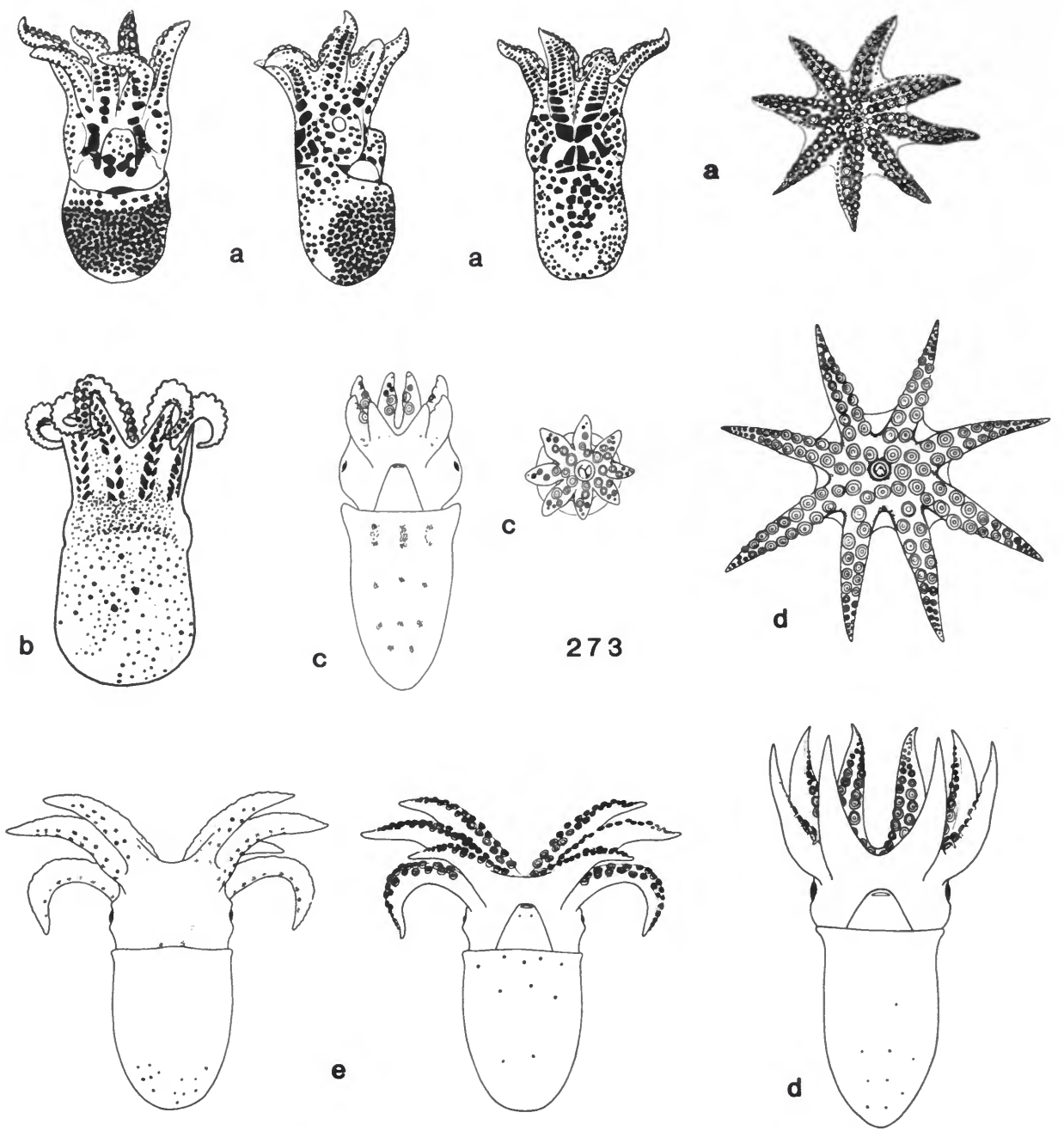

FIGURE 273.—Octopodidae, *Octopus* unidentified, Atlantic Ocean: *a*, *Octopus* sp., ventral, lateral, dorsal, and oral views, young, 5.5 mm ML, western South Atlantic (off Brazil) (from Adam, 1937); *b*, "*Octopus verrilli* var. *palliata*," dorsal view, young, 11.0 mm ML, western North Atlantic (off Bahamas) (from Robson, 1929b); *c–e*, *Octopus* spp., young, western North Atlantic (Vecchione original): *c*, oral and ventral views, 2.2 mm ML; *d*, ventral and oral views, 5.6 mm ML; *e*, dorsal and ventral views, 7.2 mm ML.

Eledone nigra (Hoyle, 1910)

SPECIES CHARACTERS.—*Young:* Hatchling stage unknown.

Larvae 6.9 mm ML (Figure 272*c*): arms subequal, 6.2 mm long with over 16 chromatophores in 1 row; funnel with 3 chromatophores on lip; dorsal mantle densely covered with 50+ large chromatophores (8–9 across); ventral mantle densely covered with 50+ smaller chromatophores; dorsal head with 6 chromatophores (4 + 2 pattern); eye chromatophore number unknown; ventral head chromatophore number and pattern unknown; visceral chromatophore number 12; silver iridophores around eyes.

Other stages in plankton not known.

GEOGRAPHICAL DISTRIBUTION.—Southeast Atlantic Ocean, South Africa.

REMARKS.—Figured under the name *Pareledone* by Rees (1954b). Voss (pers. comm.) examined the type in 1967 and concluded it is a species in the genus *Eledone*.

REFERENCES.—Rees (1954b).

UNIDENTIFIED OR UNVERIFIED MATERIAL

A number of authors have described and/or figured planktonic octopodid larvae. However, in only a few cases are characters clearly enough indicated to allow specific identification. In the preceding section on species accounts we prepared standardized descriptions and included discussions and figures of each of these species.

In all other cases the descriptions and figures are inadequate

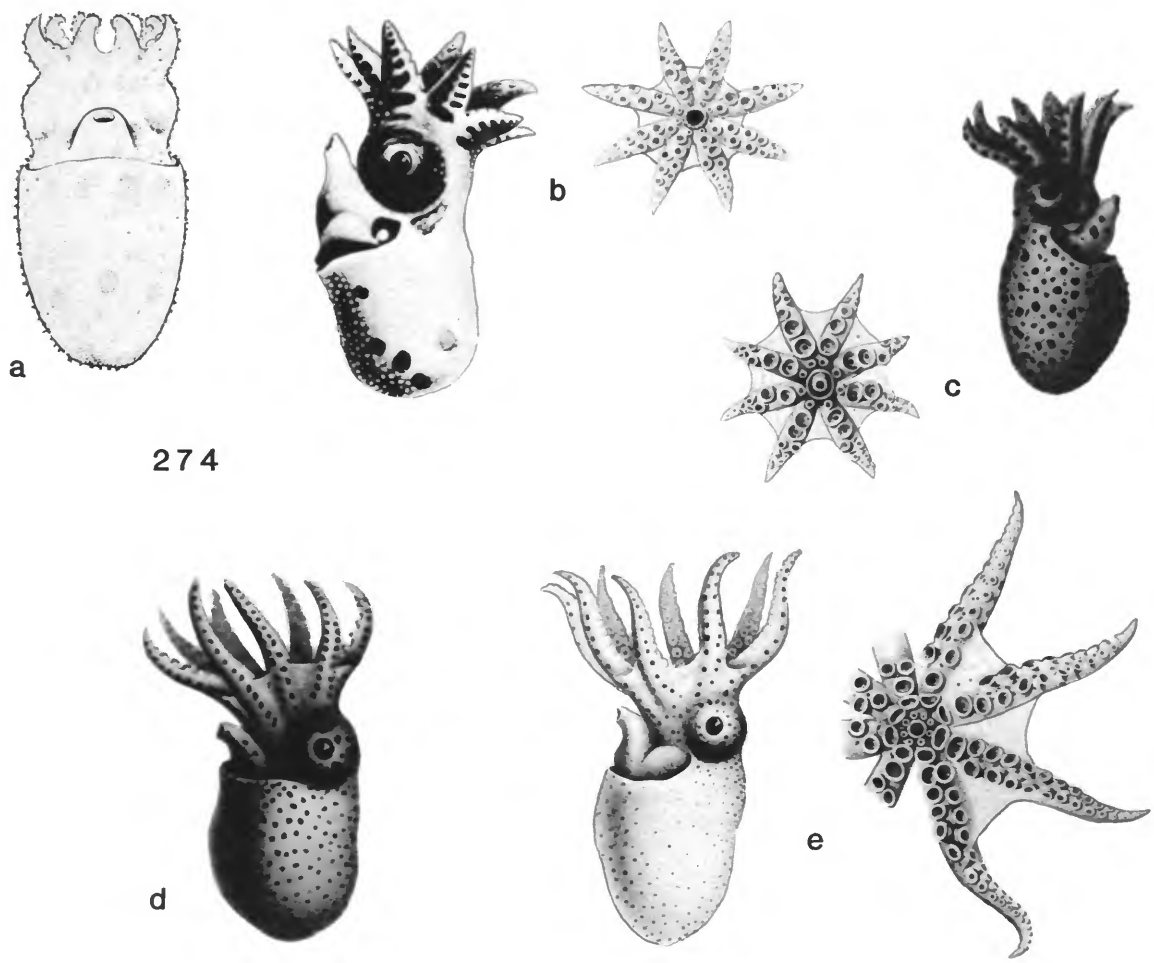

FIGURE 274.—Octopodidae, *Octopus* unidentified, Atlantic Ocean (cont.), Mediterranean and Indian Ocean: *a*, ventral view, young (possibly *O. vulgaris*), 2.6 mm ML, Mediterranean (from Rees, 1953); *b–e*, young (possibly *O. vulgaris*) (from Chun, 1915): *b*, lateral and oral views, 3.0 mm ML, South Atlantic (off W. Africa); *c*, lateral and oral views, 3.8 mm ML, Indian Ocean; *d*, lateral view, 4.6 mm ML, Bay of Bengal; *e*, lateral and oral views, 7.5 mm ML, western Indian Ocean.

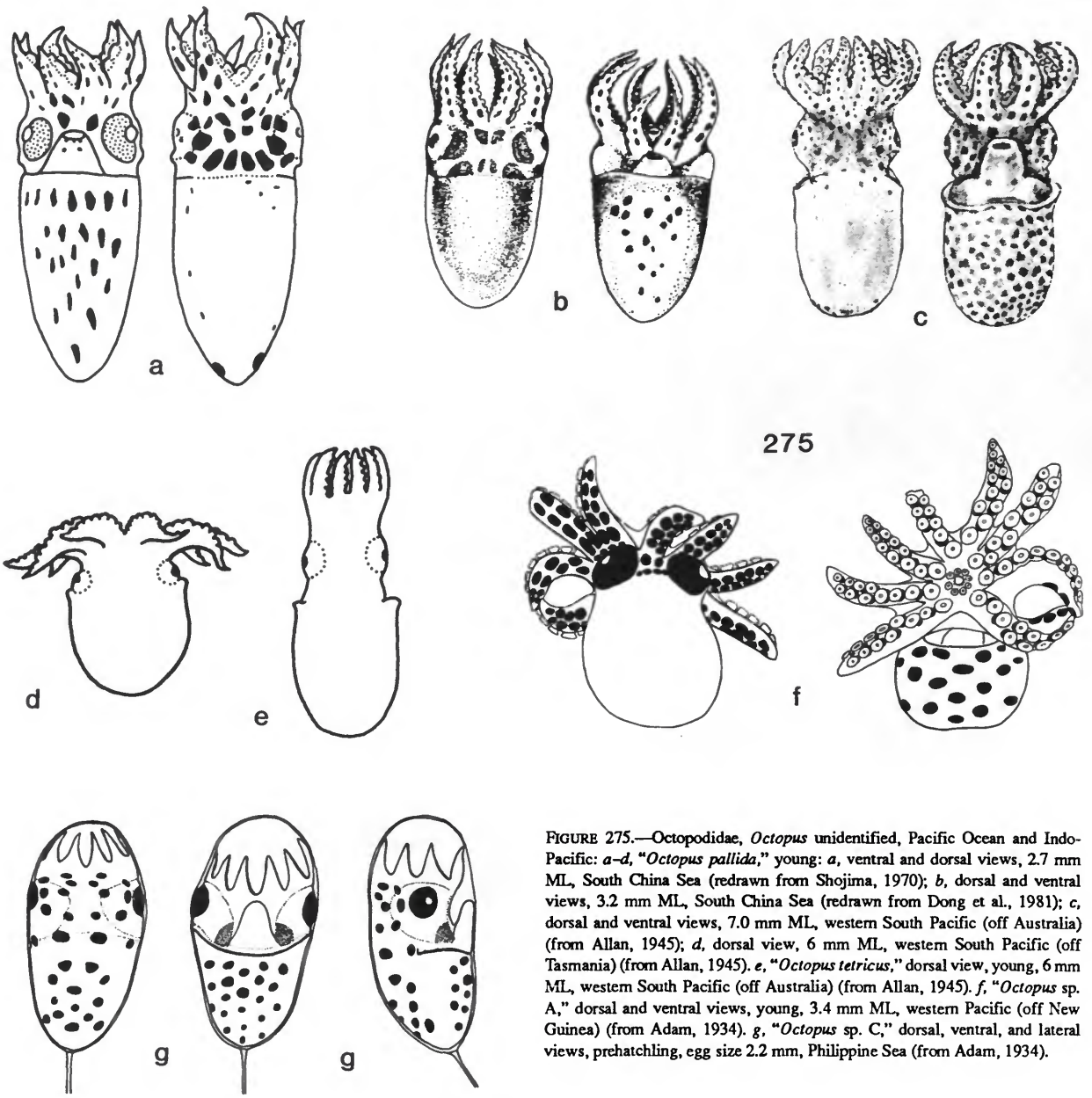

FIGURE 275.—Octopodidae, *Octopus* unidentified, Pacific Ocean and Indo-Pacific: *a–d*, "*Octopus pallida*," young: *a*, ventral and dorsal views, 2.7 mm ML, South China Sea (redrawn from Shojima, 1970); *b*, dorsal and ventral views, 3.2 mm ML, South China Sea (redrawn from Dong et al., 1981); *c*, dorsal and ventral views, 7.0 mm ML, western South Pacific (off Australia) (from Allan, 1945); *d*, dorsal view, 6 mm ML, western South Pacific (off Tasmania) (from Allan, 1945). *e*, "*Octopus tetricus*," dorsal view, young, 6 mm ML, western South Pacific (off Australia) (from Allan, 1945). *f*, "*Octopus* sp. A," dorsal and ventral views, young, 3.4 mm ML, western Pacific (off New Guinea) (from Adam, 1934). *g*, "*Octopus* sp. C," dorsal, ventral, and lateral views, prehatchling, egg size 2.2 mm, Philippine Sea (from Adam, 1934).

or the octopodid faunas of the regions represented are not well-enough known to allow the larval stages to be identified. Illustrations are included in this section of larvae whose specific identity cannot be positively determined at this time (Figures 273–277).

Descriptions of chromatophore patterns have not been included here because most specimens illustrated are post-hatchling stages in which the hatchling patterns cannot be adequately characterized. For additional information refer to the orignal references.

Information is provided here only so that workers on regional faunas will be aware of the status of knowledge of the species represented in their areas. An especially complete description and well-illustrated treatment of a regional fauna of planktonic octopodid larvae, in which a large number of unidentified but distinct species are represented, is found in the detailed paper by Young, Harman, and Hochberg (1989).

REFERENCES.—Adam (1934, 1937, 1941), Allan (1945), Berry (1914), Chun (1915), Dong, Guo, Lu, and Li (1981), Fields and Gauley (1972), Joubin (1891), Robson (1929b), Shojima (1970), Verrill (1883), Young, Harman, and Hochberg (1989).

FIGURE 276.—Octopodidae, *Octopus* unidentified, ventral and dorsal views, Hawaiian Islands: *a*, "*Octopus* type E" (possibly equals "*Octopus hawaiiensis*"), hatchling, 2.0 mm ML; *b*, "*Octopus* type I," hatchling, 1.9 mm ML; *c*, "*Octopus* type H," hatchling, 1.7 mm ML; *d*, "*Octopus* type D," hatchling, 2.1 mm ML. (From Young et al., 1989.)

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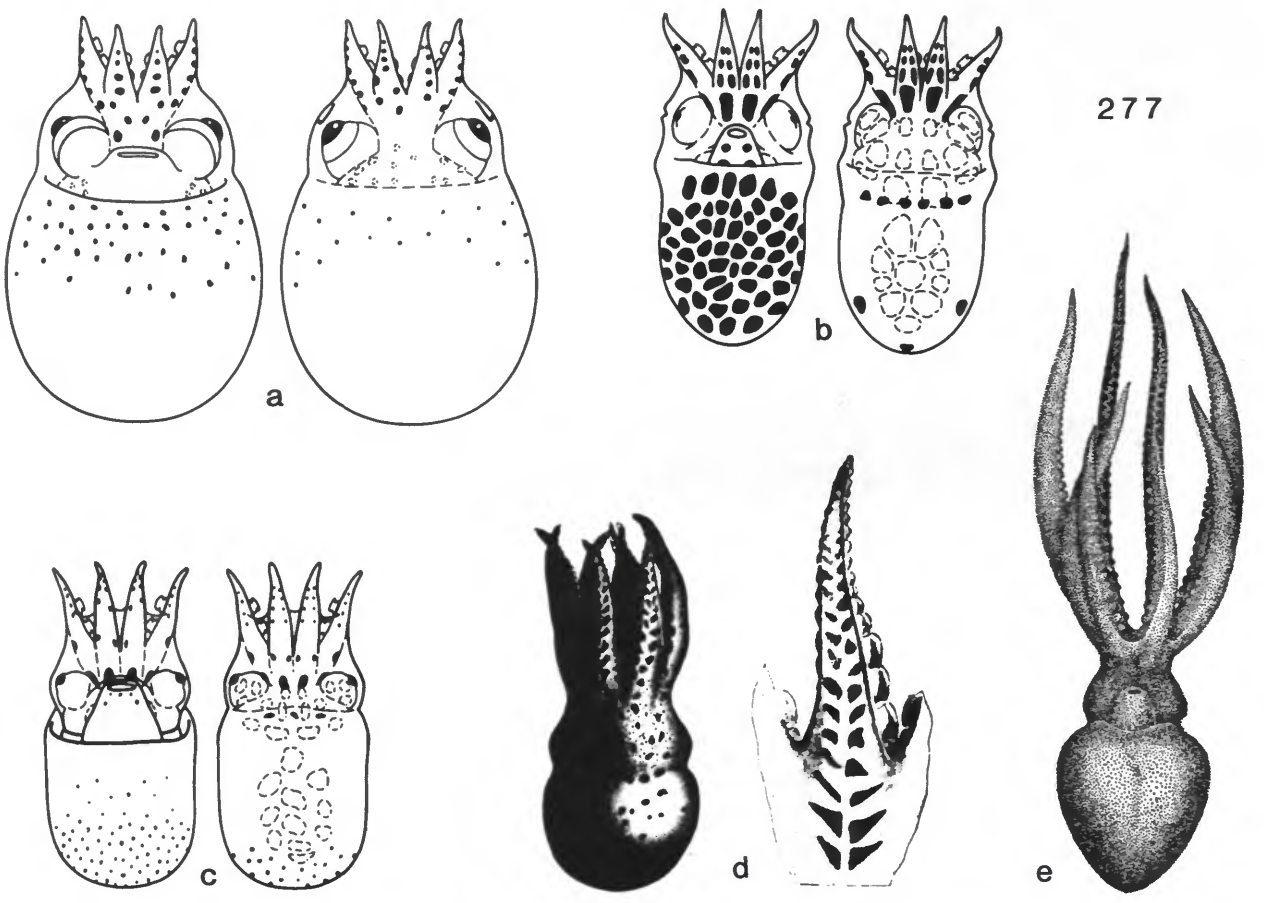

FIGURE 277.—Octopodidae, *Berrya* and *Octopus* unidentified, Hawaiian waters (cont.): *a*, "*Octopus* type G" (probably *Berrya hoylei*), ventral and dorsal views, posthatchling, 2.65 mm ML; *b*, "*Octopus* type B," ventral and dorsal views, hatchling, 2.0 mm ML; *c*, "*Octopus* type A," ventral and dorsal views, hatchling, 1.4 mm ML (*a–c*, from Young et al., 1989); *d*, "*Octopus* type beta," dorsal and aboral arm surface views, young, 4.0 mm ML; *e*, "*Octopus* type alpha" (probably *Octopus ornatus*), ventral view, young, 13.0 mm ML (*d,e*, from Berry, 1914).

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Appendix 1

Octopod Worksheet

(A, Absent; L, Left; P, Present; R, Right)

Genus/Species:
Locality:

Family:
Preservation: ETOH ISO FORM
Habitat: Shelf Slope Oceanic

ML _____ mm
TL _____ mm

Mantle shape: 

Other shape:

Mantle: Gelatinous Firm
Translucent Opaque

	Arm length right side	Sucker count	Sucker size normal	Sucker size enlarged	Sucker stalk	Sucker ornamentation
AI	_____ mm		_____ mm	_____ mm	P / A	
AII	_____ mm		_____ mm	_____ mm	P / A	
AIII	_____ mm		_____ mm	_____ mm	P / A	
AIV	_____ mm		_____ mm	_____ mm	P / A	

Web size		Web pores
A (I-I)	_____ mm	P / A
B (I-II)	_____ mm	P / A
C (II-III)	_____ mm	P / A
D (III-IV)	_____ mm	P / A
E (IV-IV)	_____ mm	P / A

Hectocotylized arm (male): R / L
Hectocotylus sac (male): P / A
Shell membrane (female): P / A
Mantle pores: P / A
Fins and Cirri: P / A
Ink sac: P / A
Outer gill lamellae count:

HL: _____ mm
HW: _____ mm
FuL: _____ mm

Eye diameter
min. _____ mm
max. _____ mm

Eye position 

Dorsal, ventral, and lateral illustrations

Dermal papillae: P / A
Koelliker's bristles: P / A
Supra-ocular cirri: P / A
Ocelli: P / A
Lateral mantle fold: P / A

	Chromatophores	Iridophores
Funnel		
ventral		
lateral		
Arms		
I		
II		
III		
IV		
Mantle		
dorsal		
ventral		
lateral		
Viscera		
dorsal		
ventral		
Head		
dorsal		
ventral		
lateral		

Comments:

Appendix 2

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