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Illustrated Embryonic Stages of the Eastern Atlantic Squid *Loligo forbesi*

by

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Abstract. The embryonic development of *Loligo forbesi* was observed from 14-day-old eggs to natural hatching. Egg strands were spawned in floating cages by wild-caught females in the Azores Islands, air-shipped to Galveston, and incubated in a closed seawater system. The period from spawning to hatching ranged from 68 to 75 days at a mean temperature of 12.5°C (SD 0.5°C). The diameters of individual eggs ranged from 3.0 to 3.1 mm and the dorsal mantle lengths of hatchlings ranged from 4.3 to 4.9 mm. The major developmental patterns were nearly identical to those of *L. vulgaris* (eastern Atlantic Ocean) and *L. pealei* (western Atlantic Ocean), except that *L. forbesi* took longer to hatch because of the larger embryos and hatchlings. The most noticeable differences in development involved the number and distribution of chromatophores. The chromatophore pattern was one of the best criteria for staging *L. forbesi* in late development.

INTRODUCTION

Loligo forbesi Steenstrup, 1856, is an eastern Atlantic Ocean species distributed from about 60°N on the coast of Norway to 20°N on the coast of northwest Africa (ROPER *et al.,* 1984) and throughout the Mediterranean Sea (MANGOLD-WIRZ, 1963). It is one of the economically important species in the English Channel (HOLME, 1974), in Scottish waters (THOMAS, 1973), in the Azores Islands (MARTINS, 1982), and off Spain and France (WORMS, 1983a). Studies to date on this species have been primarily of a taxonomic nature (ADAM, 1955) or works concerned mainly with aspects of fisheries biology (HOLME, 1974; MARTINS, 1982). Embryological observations are limited to a short note by NAEF (1928) comparing *L. forbesi* to *L. vulgaris.*

This embryological study was undertaken primarily to help predict the onset of hatching in laboratory growth studies (*e.g.,* YANG *et al.,* 1980; BOLETZKY & HANLON, 1983; HANLON *et al.,* 1985). Loliginid squids are important for biomedical experimentation (*e.g.,* NIXON & MESSENGER, 1977; TANSEY, 1979), especially the giant fibers of the peripheral nervous system (ADAMS *et al.,* 1983). *Loligo forbesi* is a particularly promising species to culture because of its large hatchling size (HANLON *et al.,* 1985).

The present paper illustrates the morphological form of post-cleavage stages in the embryonic development of *Loligo forbesi.* Criteria established by NAEF (1928) for *L. vulgaris* and ARNOLD (1965) for *L. pealei* have been used in conjunction with our observations of several additional characters, namely chromatophore pattern development (*cf.* FIORONI, 1965) and internal organ formation.

MATERIALS AND METHODS

Egg capsules were laid 28 January 1986 by captive adult female *Loligo forbesi* caught with squid jigs at a depth of 200 m near the island of Faial in the Azores Islands. The females laid their eggs in a large floating cage (2 × 3 × 2 m) in Horta harbor on Faial where the local water temperature was 14 to 16°C and the salinity 36‰. Live embryos were transported by air freight from the Azores to the Marine Biomedical Institute 11 days after spawning. Twenty-two strands of eggs were shipped in two plastic bags containing about 5 L of seawater and an equal volume of oxygen at temperatures of 12 to 15°C. Upon arrival the eggs were acclimated gradually to the conditions of the closed recirculating tank system. The egg capsules were suspended in the water column and incubated at a salinity of 34 to 35‰ and a mean temperature of 12.5°C (SD 0.5°C).

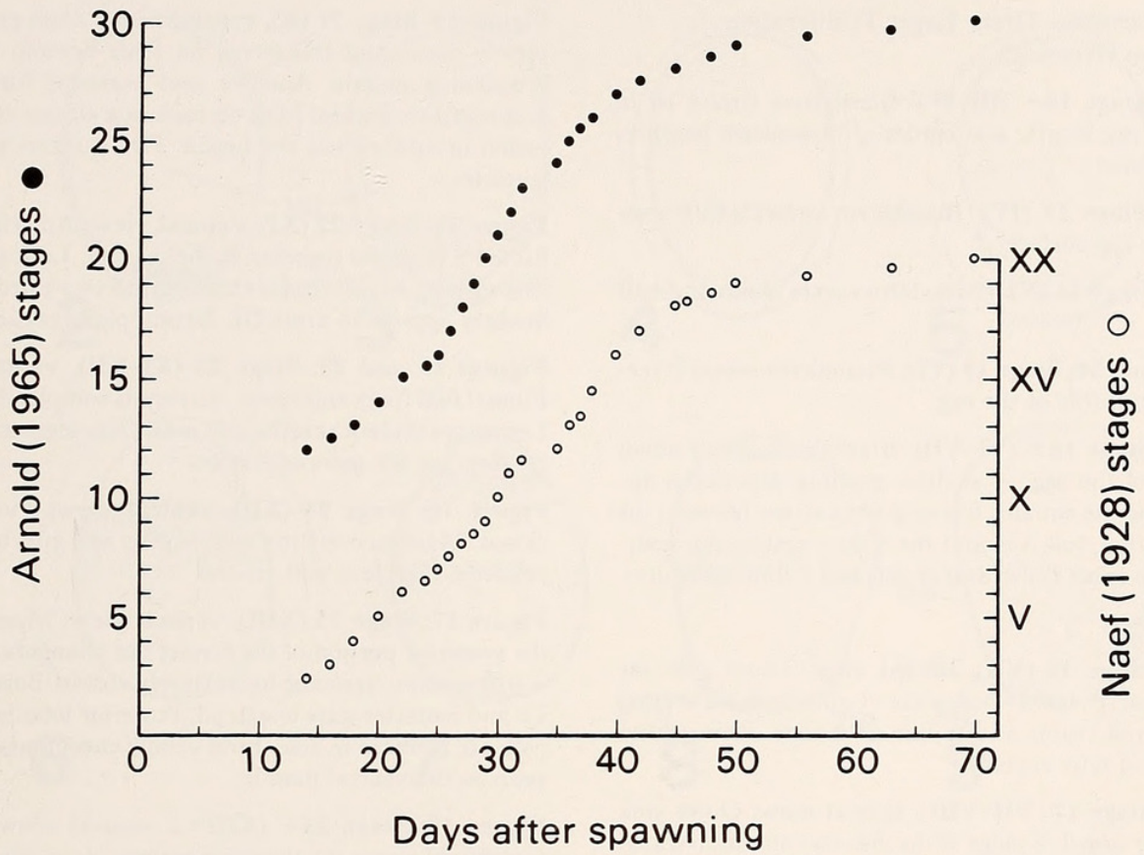

Figure 1

Embryonic development of *Loligo forbesi* in comparison to the stages proposed by ARNOLD (1965) and NAEF (1928) during the period from 14-day-old embryo to hatching. (Mean incubation temperature 12.5°C; SD 0.5°C.)

Regular observations were made from 14-day-old eggs throughout the remainder of embryonic development on four egg strings with embryos of uniform age. Representative embryos were observed carefully and drawn to scale under a dissecting microscope. All drawings were made from living embryos. In the early stages before organogenesis, embryos were observed through the chorion after careful removal of the tunic, and in older ones observations were made after removal of the chorion. The arabic stage represents the stage proposed by ARNOLD (1965) and the Roman numeral stage represents the stage proposed by NAEF (1928). Both ventral and dorsal views are given after stage 26 (XIV) (Figure 19); before that the dorsal view did not add substantially more information. Chromatophores on the fins were included in the "dorsal mantle" counts.

RESULTS

The egg capsules were transparent, soft, gelatinous, and fingerlike in shape. At the beginning of our observations (14 days after spawning), the eggs were stage 12 according to ARNOLD's (1965) scheme and stage II+ by NAEF's (1928) scheme, and each egg capsule was approximately 18 cm long and contained about 85 to 100 eggs arranged in a spiral. The diameters of the embryos ranged from 3.0 to 3.1 mm. From egg laying to day 14 in the Azores Islands, the environmental conditions were only moderately constant in the harbor for 11 days and during the 36 h of transportation to the U.S.A. The embryos took 68 to 75 days to hatch at 12.5 ± 0.5°C, with the main hatch on days 69 and 70. Figure 1 shows the developmental time of *Loligo forbesi* from day 14 to hatching according to the developmental stages of both ARNOLD (1965) and NAEF (1928).

Pre-organogenesis: Germ Layer Formation

Figure 2: Stage 12, Arnold (1965); (Stage II+), Naef (1928): Formation of the germ layer, or "gastrulation," is a complex process that begins when the margin of the blastoderm becomes two-layered as described in *Loligo pealei* (SINGLEY, 1977) and *L. vulgaris* (MARTHY, 1982), and the radial arrangement of blastocones becomes streaked. The definite separation of the blastoderm into an ectodermal and a mesendodermal germ layer is accomplished during stages 12–13 (III).

Pre-organogenesis: Germ Layer Proliferation (Blastoderm Growing)

Figure 3: Stage 13– (III–IV): Blastoderm covers 10 to 20% of the egg length, and border of blastoderm becomes sharply distinct.

Figure 4: Stage 13 (IV): Blastoderm covers about one-third of the egg surface.

Figure 5: Stage 14 (V): Blastoderm covers about one-half of the egg.

Figures 6 and 28: Stage 15 (VI): Blastoderm covers three-fifths to two-thirds of the egg.

Figure 7: Stage 15+ (VI–VII): Blastoderm covers about four-fifths of the egg. A shallow girdling depression appears around the equator forming a boundary between the future external yolk sac and the future embryonic body. The chorion is not illustrated in this and following figures.

Organogenesis

Figure 8: Stage 16 (VII), lateral view: Outer yolk sac envelope nearly closed. Primordia of optic vesicles are rudimentary and visible as disc-like elevations. Primordium of shell gland now visible.

Figure 9: Stage 17 (VII–VIII), lateral view: Outer yolk sac envelope closed. A ridge of the disc-like elevation transforms into a fold in the ventral area and forms a ridge in the dorsal part that becomes the optic vesicle. Border of the shell gland elevated slightly. Primordia of arms and tentacles first visible.

Figure 10: Stage 18 (VIII), lateral view: The disc-like fold entirely surrounds prospective retina and starts growing over it. Primordia of statocysts appear. Arms and tentacles grow and begin to project.

Figure 11: Stage 19 (VIII–IX), ventral view: Closure of the optic vesicle is progressing. Other organ primordia become prominent, such as gills and anal knoll.

Figure 12: Stage 20 (IX), ventral view: Opening of the optic vesicle closes. Shell gland invagination is progressing. Posterior and anterior funnel folds extend towards the midline.

Figure 13: Stage 21 (X), ventral view: Shell gland completely closes and transverse fin folds develop upon the broadening mantle. Anterior and posterior funnel folds fuse together. Funnel folds on each side elevate clearly but fusion in midline has not begun. First suckers appear on tentacles.

Figure 14: Stage 22 (XI), ventral view: Anterior part of funnel fold comes together at the margin. Lens primordia first visible. Mantle covers one-half to two-thirds of gills. Suckers appear on arms III. Retina pigmentation begins.

Figures 15 and 29: Stage 23 (XI–XII), ventral view: Funnel fold fuses anteriorly. Statocysts completely formed. Lenses are evident as refractive rods. Gills segmented clearly, showing six pairs of leaflets.

Figure 16: Stage 24 (XII), ventral view: Funnel tube closed. Mantle covers the anal papilla and gills but funnel retractor muscle is still visible.

Figure 17: Stage 25 (XIII), ventral view: Mantle covers the posterior portion of the funnel but triangular opening is still evident. Systemic heart clearly visible. Bases of arms IV and tentacles start to extend. Posterior lobes of internal yolk sac increase in size. First yellow chromatophores appear on the ventral mantle.

Figure 18: Stage 25+ (XIII+), ventral view: Mantle completely covers the posterior margin of the funnel. Ventral mantle chromatophores increase in number. First chromatophores are visible on tentacles; these appear to be dark reddish from the beginning.

Figure 19: Stage 26 (XIV), dorsal (left) and ventral (right) views: Ventral arm bases (the ventral component of the future primary lid) cover about one-half of the optic ganglia. Ink sac is first visible but no ink is present. Retina color is brilliant reddish. Chromatophores are first visible on the ventral and dorsal sides of head, the dorsal mantle and fins, and the fourth arms.

Figure 20: Stage 27 (XVI), dorsal (left) and ventral (right) views: Ventral arm bases extend into a primary lid and the edge reaches posterior end of eye vesicle. Ink sac fills with ink. Anus structure clearly visible with conspicuous anal papillae or flaps.

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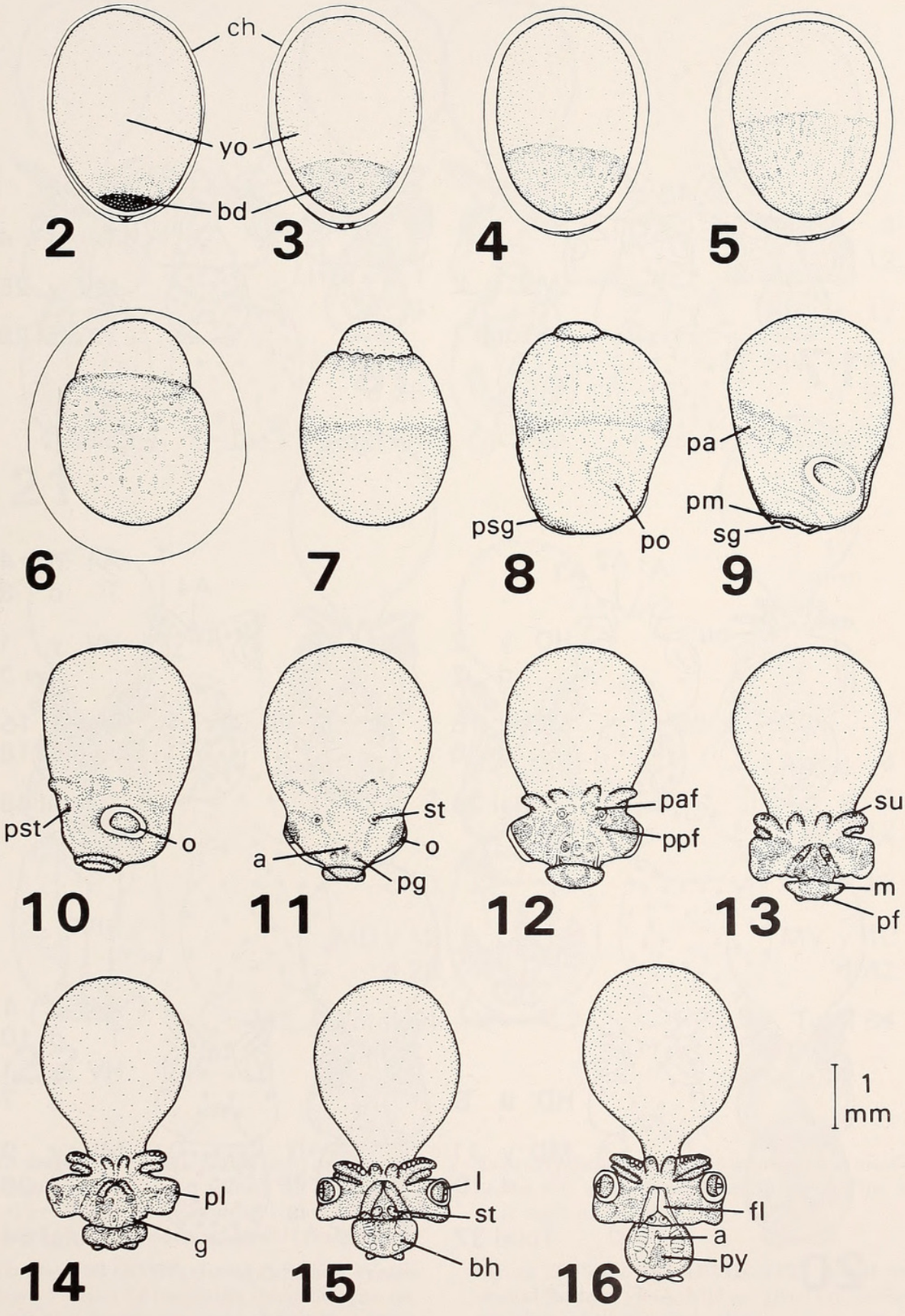
Explanation of Figures 2 to 27

Embryonic development of *Loligo forbesi*, from germ layer formation to newly hatched squid. See Results for details of each Figure. Key to abbreviations: a, anal knoll; ap, anal papilla or flaps; bd, blastoderm; bh, branchial heart; bu, buccal mass; c, caecum; ch, chorion; co, cornea; d, dark reddish chromatophore; ft, funnel tube; g, gill; h, Hoyle's Organ; is, ink sac; iy, internal yolk; l, lens; m, mantle; mg, mid-gut gland; o, optic vesicle; og, optic ganglion; op, olfactory plate; pa, primordia of arms; paf, primordium of anterior funnel fold; pf, primordium of fin; pg, primordium of gill; pl, primordium of lens; pm, primordium of mantle; po, primordium of optic vesicle; ppf, primordium of posterior funnel fold; psg, primordium of shell gland; pst, primordium of statocyst; py, posterior lobes of internal yolk sac; sg, shell gland; sh, systemic heart; sm, stomach; st, statocyst; su, sucker; y, yellow chromatophore; yo, yolk; A1, arm I; A2, arm II; A3, arm III; A4, arm IV; T, tentacle; HD, dorsal side of head; HV, ventral side of head; MD, dorsal side of mantle; MV, ventral side of mantle.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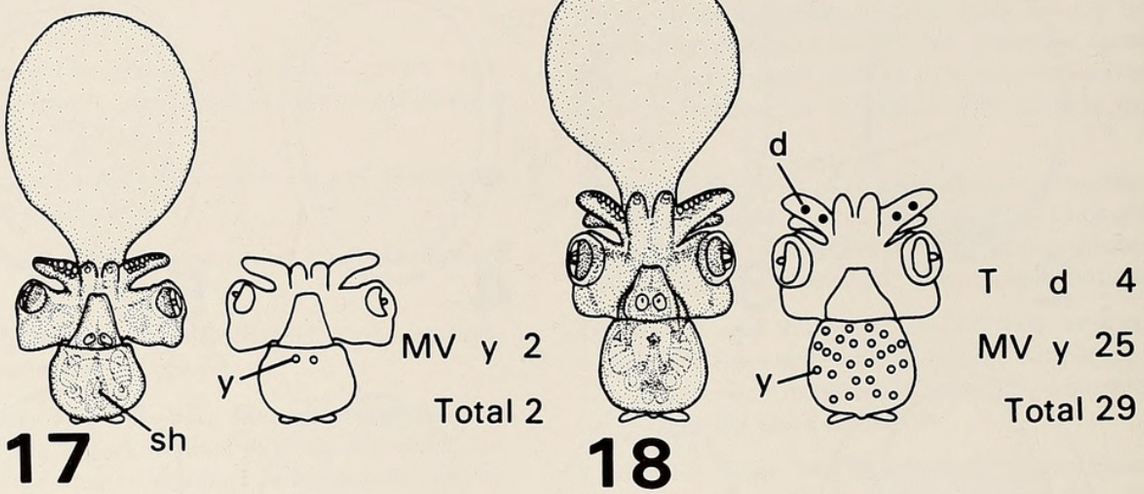
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Total 29
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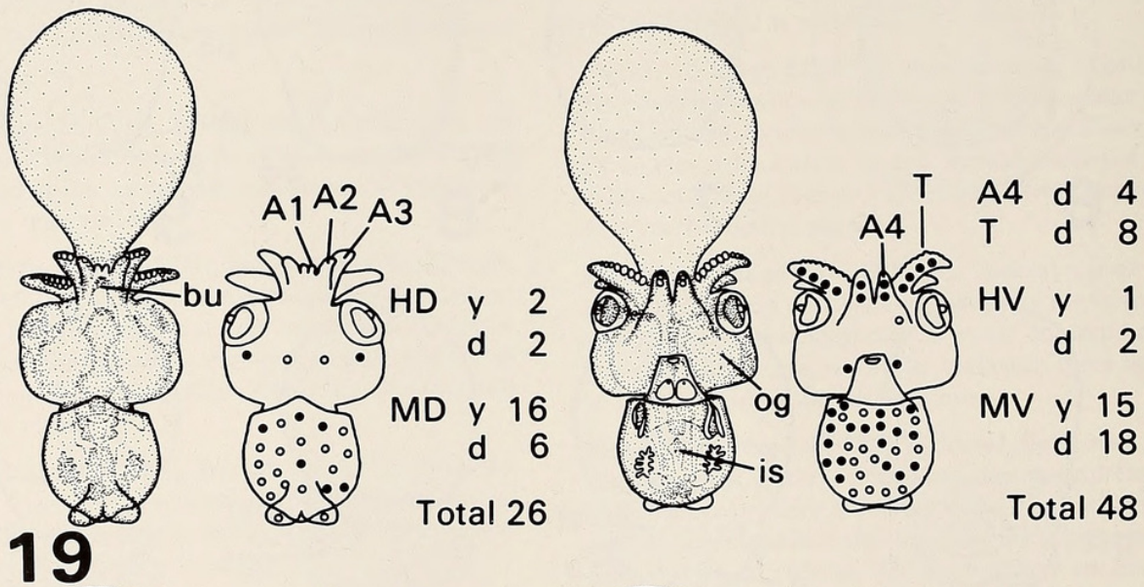
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HD y 2
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MV y 15
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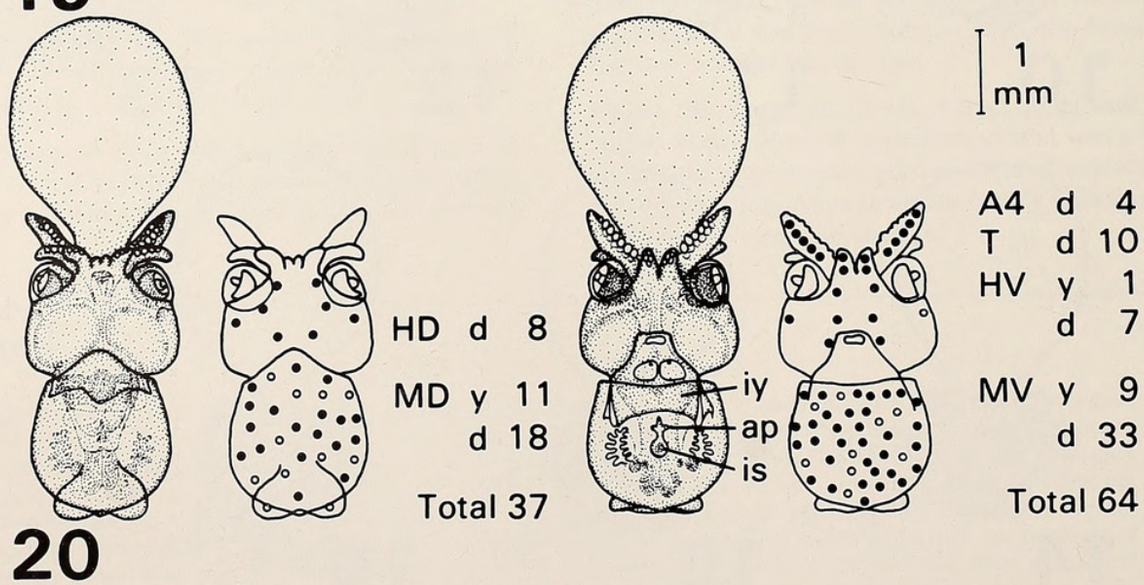
Total 48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MD y 11
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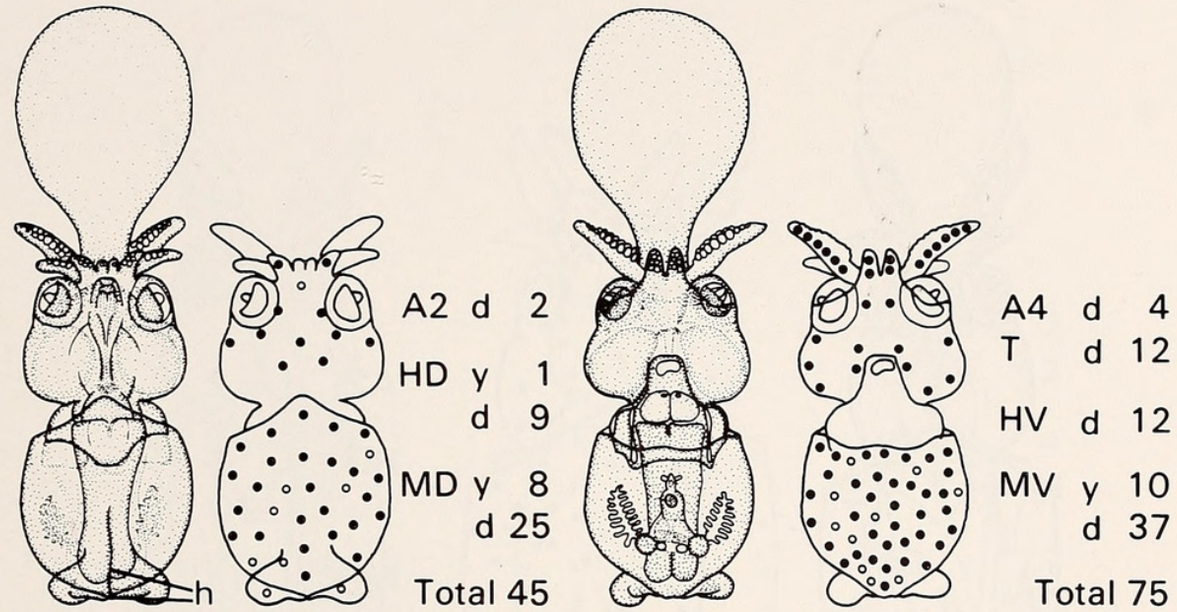
Total 64



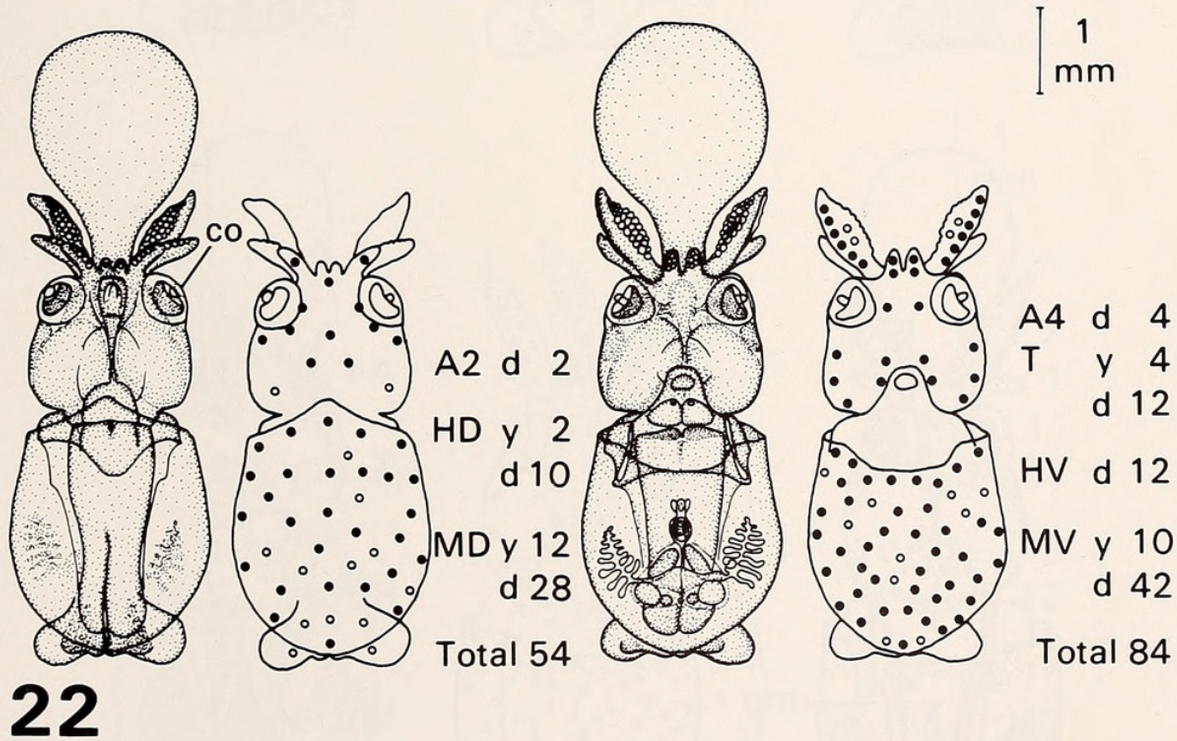
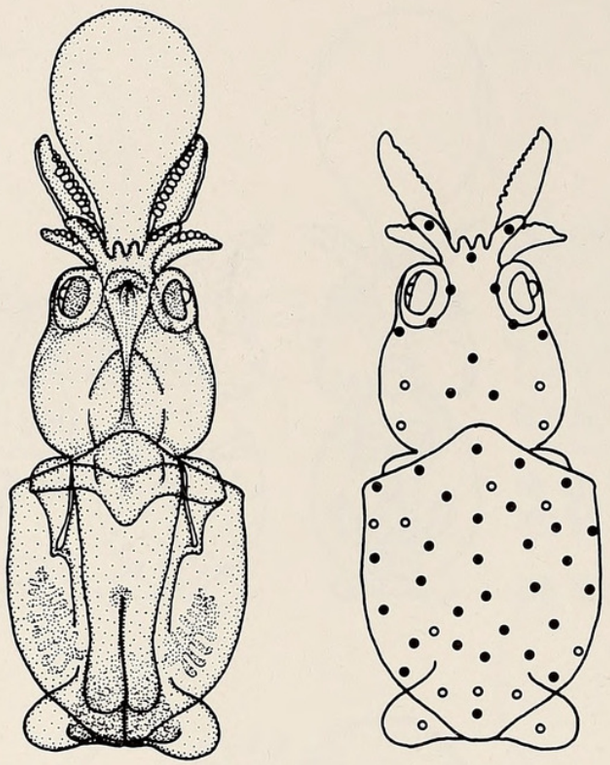


Figure 21: Stage 27+ (XVII), dorsal (left) and ventral (right) views: The edge of the primary lid covers about one-half of eye vesicle. Hoyle's organ is first visible on dorsal mantle. Chromatophores on arms II first appear.

Figure 22: Stage 28 (XVIII), dorsal (left) and ventral (right) views: Primary lid completely covers the optic vesicle and part of it transforms into a transparent cornea. External yolk sac approximately same size as mantle length. Second row of chromatophores appears on the tentacles; these begin as yellows.

Figure 23: Stage 28+ (XVIII–XIX), dorsal (top) and ventral (bottom) views: Mid-gut gland first visible around the internal yolk sac. Stomach and caecum first visible.



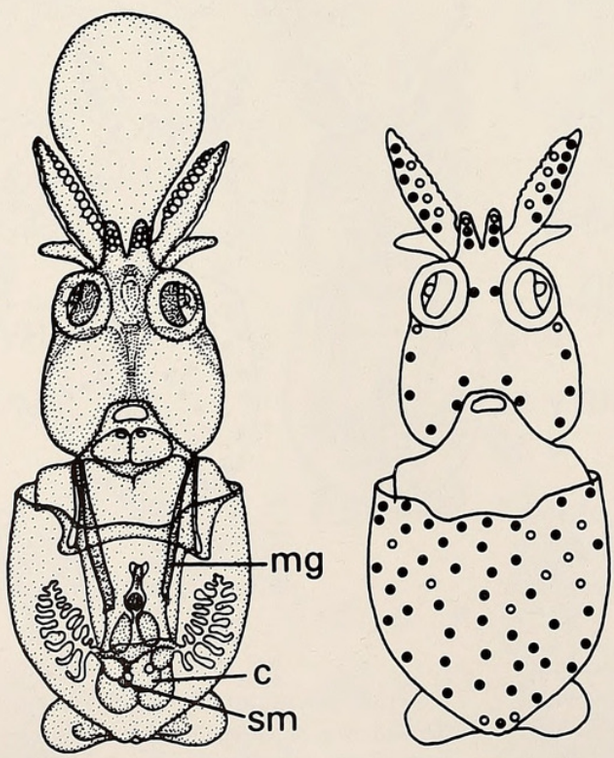
A2 d 2

HD y 4
d 10

MD y 11
d 30

Total 57

1 mm



A4 y 2
d 4

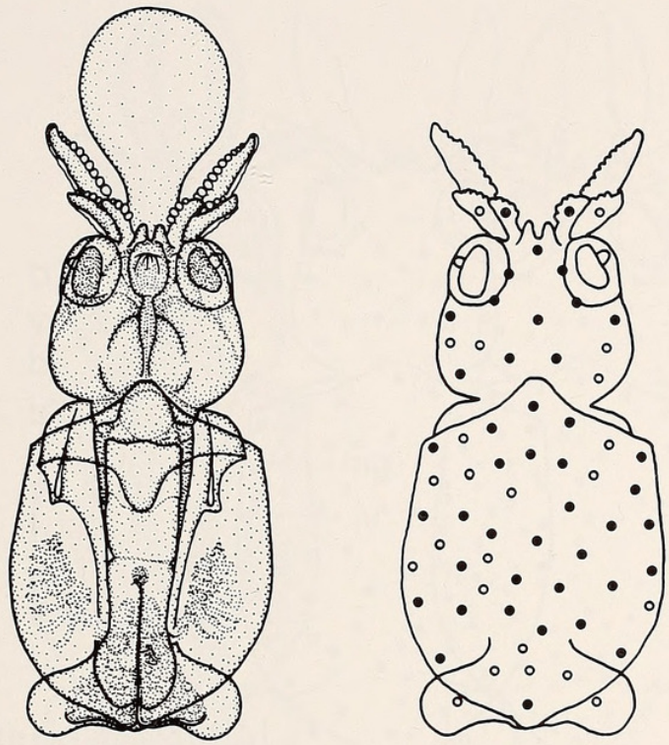
T y 8
d 12

HV y 2
d 12

MV y 10
d 44

Total 94

23



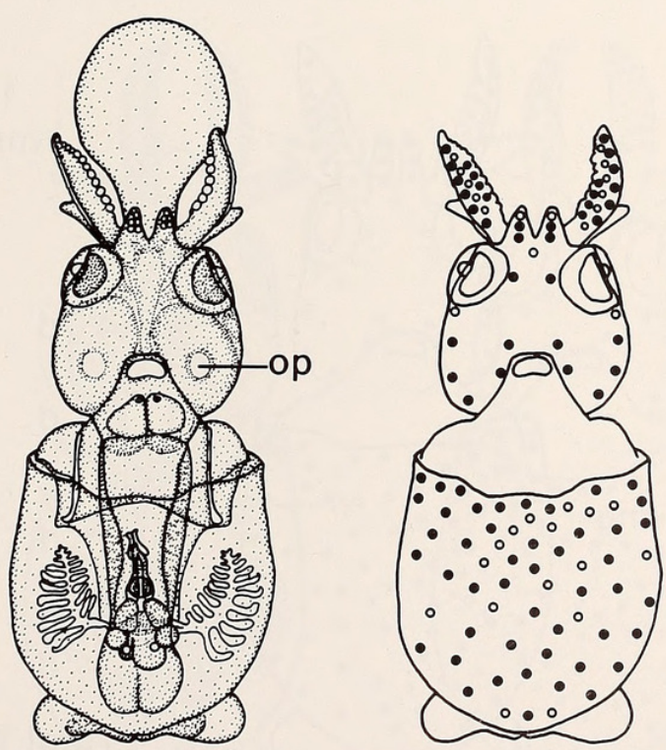
A2 d 2
A3 y 2

HD y 4
d 11

MD y 17
d 30

Total 66

1 mm



A4 y 2
d 4

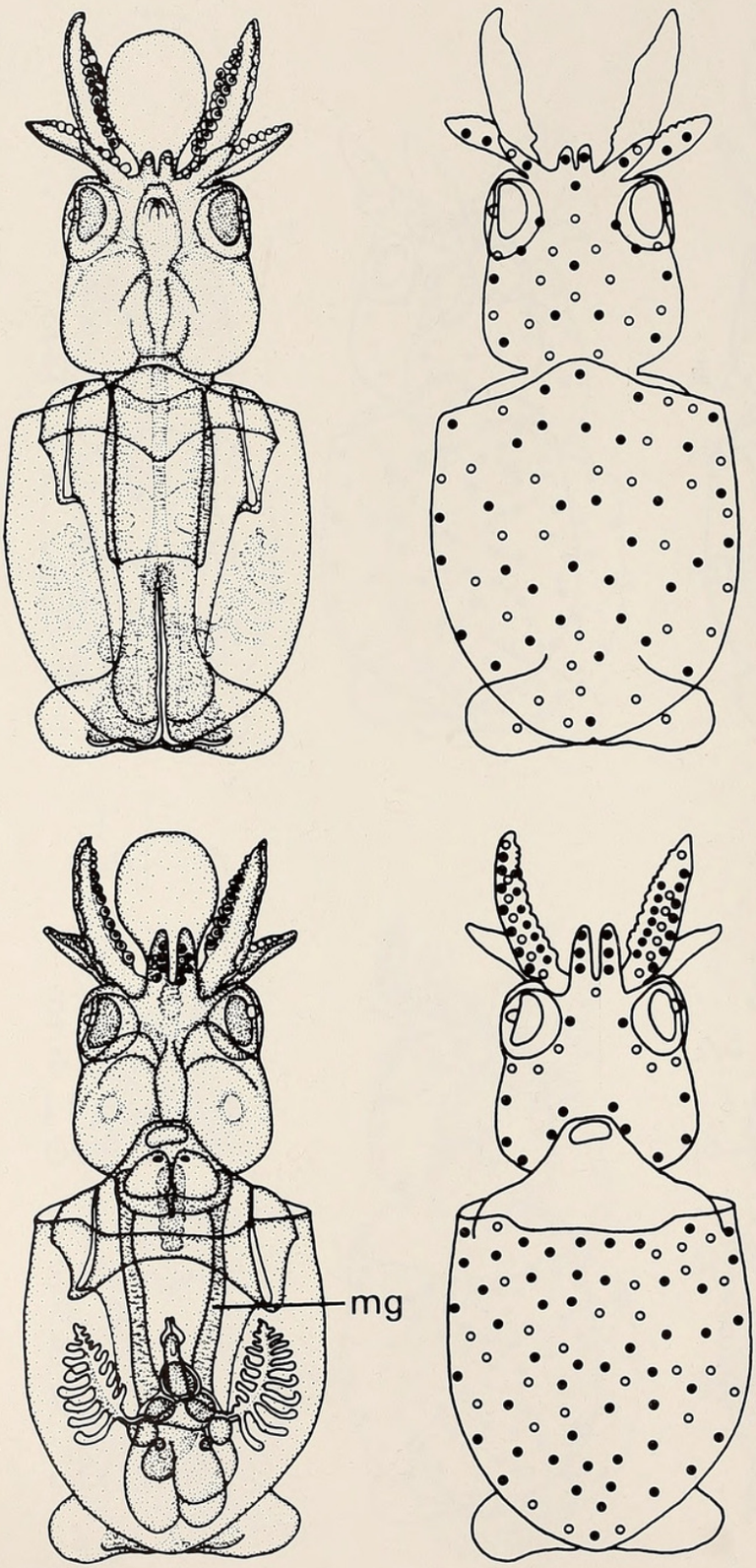
T y 11
d 20

HV y 3
d 12

MV y 16
d 47

Total 115

24

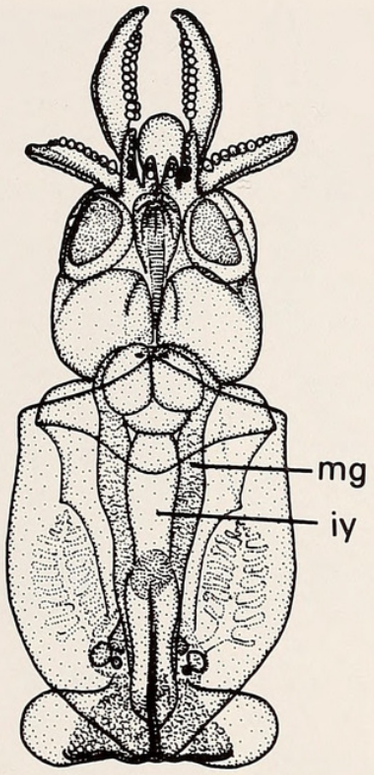


A1	d	2
A2	y	2
	d	2
A3	d	4
HD	y	14
	d	12
MD	y	28
	d	34
Total		98

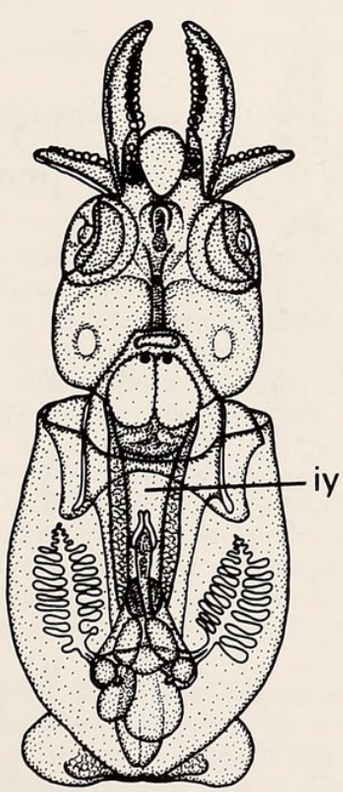
1 mm

A4	d	6
T	y	14
	d	28
HV	y	7
	d	12
MV	y	26
	d	50
Total		143

25



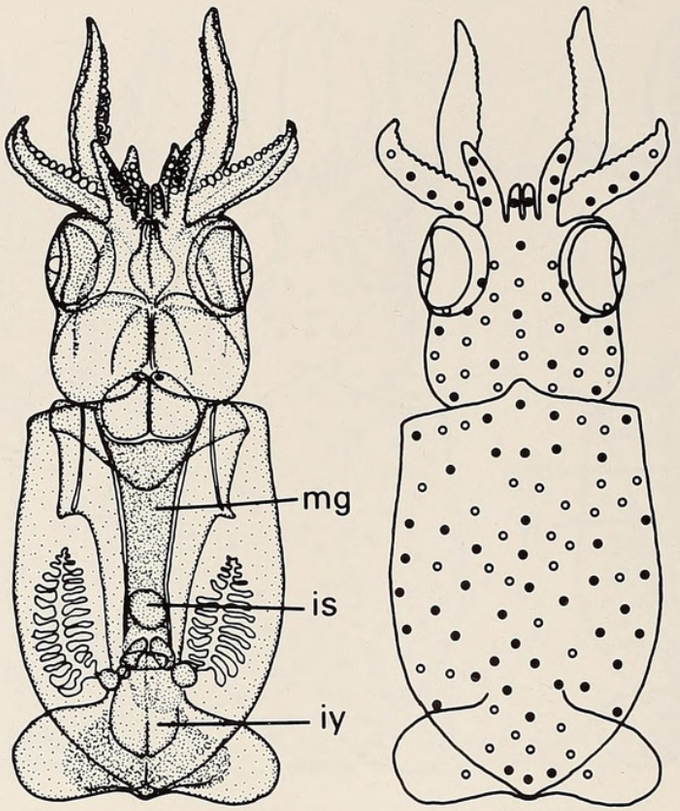
A1	d	2
A2	y	2
	d	4
A3	y	2
	d	4
HD	y	17
	d	12
MD	y	30
	d	43
Total		116



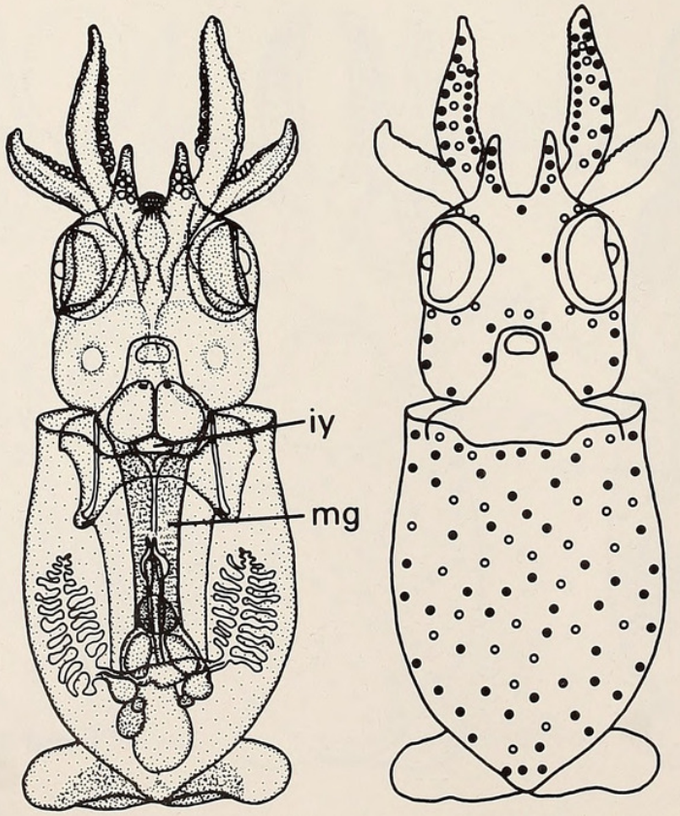
1 mm

A4	y	2
	d	6
T	y	12
	d	32
HV	y	10
	d	13
MV	y	26
	d	53
Total		154

26



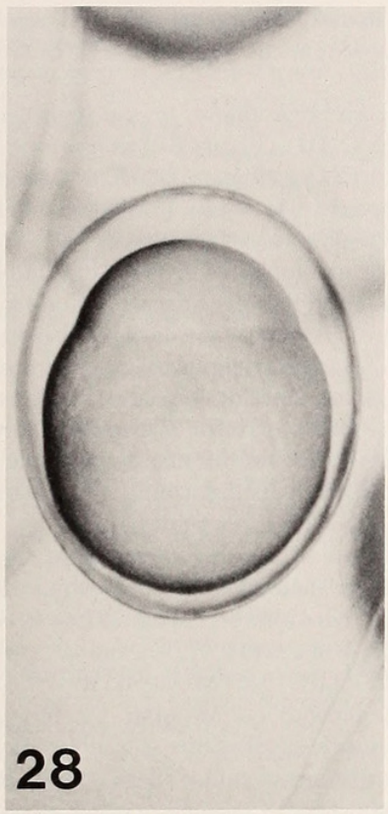
A1	d	2
A2	d	6
A3	y	2
	d	6
HD	y	21
	d	12
MD	y	33
	d	45
Total		127

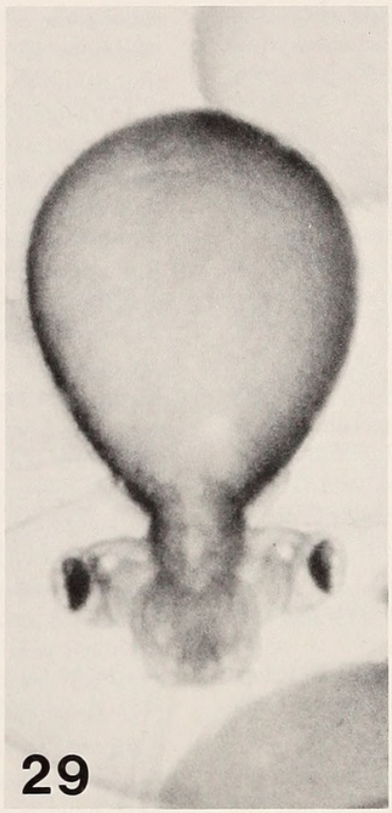


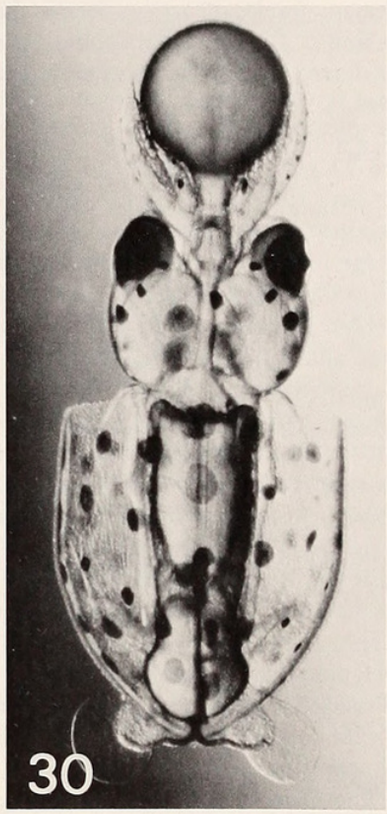
1 mm

A4	y	2
	d	6
T	y	12
	d	33
HV	y	12
	d	13
MV	y	27
	d	54
Total		159

27







Explanation of Figures 28 to 30

Figure 28. Photograph of embryo at stage 15 (VI). Compare Figure 6.

Figure 29. Photograph of embryo at stage 23 (XI–XII). Compare Figure 15.

Figure 30. Photograph of embryo at stage 29 (XIX). Compare Figure 24.

Figures 24 and 30: Stage 29 (XIX), dorsal (top) and ventral (bottom & Figure 30) views: Third row of chromatophores appears on tentacles; these are small and red from the start. First chromatophores appear on arms III. The primordia of the olfactory organ are clearly visible on the ventral head as thickenings of the epidermis.

Figure 25: Stage 29+ (XIX+), dorsal (top) and ventral (bottom) views: Internal yolk sac begins to be absorbed and decreases in size. Mid-gut gland develops around the internal yolk sac. The external yolk sac approximately equal in length to tentacle length. First chromatophores and suckers appear on arms II.

Figure 26: Stage 29++ (XIX–XX), dorsal (top) and ventral (bottom) views: The external yolk sac is approximately equal to length of arms II. Internal yolk sac reduced in size. Caecum and stomach increase in size. In some embryos, the external yolk sac may be lost and premature hatching may occur. Dark chromatophore patterns on both dorsal and ventral head remain the same until hatching.

Figure 27: Stage 30 (XX), dorsal (top) and ventral (bottom) views: Newly hatched squid. Hoyle's organ depleted. Internal yolk sac visible dorsally and reduced to a small triangular body. External yolk almost absorbed and only yolk sac envelope remains. External yolk sac sometimes lost just after hatching. Hatching size ranged from 4.3 to 4.9 mm ML, with a mean of 4.6 mm ML (SD 0.1 mm).

DISCUSSION

The life history of *Loligo forbesi* is known only in general terms (*e.g.*, HOLME, 1974; MARTINS, 1982) and this study plus our laboratory culture experiments (*e.g.*, HANLON *et al.*, 1985) are meant to fill some of the gaps. Details of development may also help distinguish *L. forbesi* from the closely related *L. vulgaris*, with which it shares many morphological features and also overlaps in distribution (ROPER *et al.*, 1984).

For embryological study, among the best-known cephalopods are *Loligo vulgaris* and *L. pealei*, for which detailed staging schemes were established by NAEF (1928) and ARNOLD (1965) respectively. Although there are some dif-

ferences in developmental processes between these two species and *L. forbesi,* Arnold's and Naef's schemes could be transferred directly to the developmental sequence of *L. forbesi.*

The sigmoid developmental pattern of *Loligo forbesi* (Figure 1) was very similar to other species of *Loligo* (Boletzky, 1974:fig. 1) but a little different from that reported for *L. pealei* (Arnold, 1965), whose development after stage 12 was approximately linear. *Loligo forbesi* has large eggs that are deposited in cold water. Individual eggs of *L. forbesi* spawned in the Azores were 3.0–3.1 mm in diameter and represent the largest known egg of *Loligo* spp.: *L. opalescens* 2.0–2.5 mm (Fields, 1965), *L. vulgaris* 2.3–2.7 mm (Worms, 1983b), and *L. pealei* 1.0–1.6 mm (Summers, 1983). As a result, the eggs develop more slowly than other *Loligo* species. It took 68–75 days at 12.5°C for *L. forbesi* compared to 10–27 days at 12–23°C for *L. pealei* (McMahon & Summers, 1971), 30–35 days at 13.6°C for *L. opalescens* (McGowan, 1954), and 45–70 days at 12–14°C for *L. vulgaris* (Mangold-Wirz, 1963; Boletzky, 1974).

Development is a continual process, but the developmental "stages" have been determined arbitrarily. Thus, identification of a particular stage is sometimes difficult. In each case several stages are divisible into two or more steps. The "ideal" staging criteria suggested by Naef (1928), and partially reconsidered by Arnold (1965, 1974), follow morphological events throughout embryogenesis (*e.g.,* easily recognizable steps in eye and shell gland closure, funnel formation, eye lid growth, *etc.*) and are useful in *Loligo forbesi* as well. Progressive closure of the optic vesicle, as described for *L. vulgaris* (Marthy, 1973) and *L. pealei* (Arnold & Williams-Arnold, 1978), is a good indicator for stages 16–20 (VII–IX). The process of funnel folding (Arnold *et al.,* 1978) and of formation of the primary lid over the eye (Naef, 1928; Arnold, 1984) are excellent criteria for stages 20–24 (IX–XII) and stages 25–28 (XIII–XVIII) respectively. The proportions among some internal organs such as internal yolk sac, mid-gut gland, stomach, caecum, and ink sac change rapidly from stages 28 to 30 (XVIII to XX), but their size and position are good staging criteria.

We distinguish yellow from dark chromatophores because nearly all chromatophores in the embryo begin as yellows and transform into a darker (red-brown) pigment with time (*e.g.,* Fioroni, 1965; Forsythe & Hanlon, 1985; Packard, 1985). This progression can be seen in the figures and is useful in staging. The third (inner) row of chromatophores to form on the tentacles at stage 29 (XIX) (Figure 24) are an exception; they start as dark reddish and are conspicuously smaller chromatophore organs, and this appears to be characteristic of *Loligo* spp. hatchlings (*e.g.,* Fioroni, 1965; McConathy *et al.,* 1979). There appears to be no "standard color" of the dark chromatophores at hatching; unpublished data of Hanlon and Boletzky show that some year-classes of *L. forbesi* have red, and some have brown, dark chromatophores. Thus, color alone is not useful in characterizing the species; furthermore, in preservation the colors are not usually distinguishable.

In *Loligo forbesi,* chromatophores on the ventral surface appear at stage 25 (XIII) (Figure 17) and on the dorsal surface at stage 26 (XIV) (Figure 19). These are earlier than those of *L. pealei* (Arnold, 1965) and later than those of *L. vulgaris* (Fioroni & Meister, 1974). After first appearance, chromatophores increase in number and distribution on the head, mantle, fins, arms, and tentacles. The chromatophores (especially the dark reddish ones that are easier to see) on the head, tentacles, and arms are one of the best criteria for determining later developmental stages in *L. forbesi.* There is considerable variation in the pattern of chromatophores on the mantle; thus the use of mantle chromatophores in distinguishing this species from the sympatric *L. vulgaris* will be minimal.

Size of *Loligo forbesi* at hatching ranges from 4.3 to 4.9 mm ML and is larger than other species such as *L. pealei* (about 1.8 mm ML; McConathy *et al.,* 1979), *L. vulgaris* (about 3 mm ML; Boletzky, 1979), and *L. opalescens* (2.5–3.2 mm ML; Fields, 1965; McConathy *et al.,* 1979). Size of hatchlings depends largely upon the size of eggs spawned. In laboratory experiments (unpublished observations), larger hatchlings of squids like *L. forbesi* usually have more successful attacks on food organisms and have better survival rates than smaller hatchlings like *L. pealei.* This suggests that *L. forbesi* has a different way of optimizing survival during its initial life-history stages: the large hatchlings are already a size that takes other *Loligo* hatchlings several weeks to attain, and they can feed immediately on a wide size range and diversity of food organisms (from approximately 0.8 mm to 3.5 mm long; Hanlon *et al.,* submitted). Thus, it should be relatively easier to rear *L. forbesi* in captivity during the first critical month (*e.g.,* Yang *et al.,* 1986) when mortality is generally very high.

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LITERATURE CITED

Adam, W. 1955. Résultats scientifiques des campangnes de la "Calypso." I. Campagne en Mer Rouge. VI. Cephalopodes. Annales Institut Oceanographique 30:185–195.

ADAMS, D. J., K. TAKEDA & J. A. UMBACH. 1983. Metabolic inhibitors and lithium depress synaptic transmission at the squid giant synapse. Jour. Physiol. 345:147 pp.

ARNOLD, J. M. 1965. Normal embryonic stages of the squid, *Loligo pealii* (Lesueur). Biol. Bull. 128:23–32.

ARNOLD, J. M. 1974. Embryonic development. Pp. 24–49. *In:* J. M. Arnold, W. C. Summers, D. L. Gilbert, R. S. Manalis, N. W. Daw & R. J. Lasek (eds.), A guide to laboratory use of the squid *Loligo pealei.* Marine Biological Laboratory: Woods Hole, Massachusetts.

ARNOLD, J. M. 1984. Closure of the squid cornea: a muscular basis for embryonic tissue movement. Jour. Exper. Zool. 232:187–195.

ARNOLD, J. M. & L. D. WILLIAMS-ARNOLD. 1978. Preliminary studies on the closure of the optic vesicle of *Loligo pealei* embryos. Biol. Bull. 155:426 (abstract).

ARNOLD, J. M., L. D. WILLIAMS-ARNOLD & V. PETERS. 1978. Fusion of tissue masses in embryogenesis—a scanning electron microscope and transmission electron microscope study of funnel development in the squid *Loligo pealei.* Develop. Biol. 65:155–170.

BOLETZKY, S. v. 1974. The larvae of Cephalopoda: a review. Thalassia Jugosl. 10(1/2):45–76.

BOLETZKY, S. v. 1979. Observations on the early post-embryonic development of *Loligo vulgaris* (Mollusca, Cephalopoda). Rapport de la Commission Internationale Pour la Mer Mediterranee 25/26(10):155–158.

BOLETZKY, S. v. & R. T. HANLON. 1983. A review of the laboratory maintenance, rearing and culture of cephalopod molluscs. Mem. Natl. Mus. Victoria 44:147–187.

FIELDS, W. G. 1965. The structure, development, food relations, reproduction and life history of the squid *Loligo opalescens* Berry. Calif. Dept. Fish & Game, Fish. Bull. 131: 1–108.

FIORONI, P. 1965. Die embryonale Musterentwicklung bei einigen Mediterranean Tintenfischarten. Vie et Milieu, Serie A: Biologie Marine 16:654–756.

FIORONI, P. & G. MEISTER. 1974. Embryologie von *Loligo vulgaris* Lam. Gemeiner Kalmar. Gustav Fischer Verlag: Stuttgart. Grosses Zoologisches Praktikum, Heft 16 c/2. 69 pp.

FORSYTHE, J. W. & R. T. HANLON. 1985. Aspects of egg development, post-hatching behavior, growth and reproductive biology of *Octopus burryi* Voss, 1950 (Mollusca, Cephalopoda). Vie et Milieu 35(3/4):273–282.

HANLON, R. T., R. F. HIXON, P. E. TURK, P. G. LEE & W. T. YANG. 1985. Behavior, feeding and growth of young *Loligo forbesi* (Cephalopoda: Myopsida) reared in the laboratory. Vie et Milieu 35(3/4):247 (abstract).

HANLON, R. T., W. T. YANG, P. E. TURK, P. G. LEE & R. F. HIXON. Submitted. Laboratory culture of the eastern Atlantic squid *Loligo forbesi.* Aquaculture and Fisheries Management.

HOLME, N. A. 1974. The biology of *Loligo forbesi* Steenstrup (Mollusca: Cephalopoda) in the Plymouth area. Jour. Mar. Biol. Assoc. U.K. 54:481–503.

MANGOLD-WIRZ, K. 1963. Biologie des Céphalopodes benthiques et nectoniques de la Mer Catalane. Vie et Milieu, Suppl. No. 13:285 pp.

MARTHY, H.-J. 1973. An experimental study of eye development in the cephalopod *Loligo vulgaris*: determination and regulation during formation of the primary optic vesicle. Jour. Embryol. Exper. Morphol. 29:347–361.

MARTHY, H.-J. 1982. The cephalopod egg, a suitable material for cell and tissue interaction studies. Pp. 223–233. *In:* M. M. Burger & R. Weber (eds.), Progress in clinical biological research. Vol. 85. Allan R. Liss Publishers: New York.

MARTINS, H. R. 1982. Biological studies of the exploited stock of *Loligo forbesi* (Mollusca: Cephalopoda) in the Azores. Jour. Mar. Biol. Assoc. U.K. 62:799–808.

MCCONATHY, D. A., R. T. HANLON & R. F. HIXON. 1979. Chromatophore arrangements of hatchling loliginid squids (Cephalopoda, Myopsida). Malacologia 19(2):279–288.

MCGOWAN, J. A. 1954. Observations on the sexual behavior and spawning of the squid, *Loligo opalescens,* at La Jolla, California. Calif. Dept. Fish & Game 40:47–54.

MCMAHON, J. & W. C. SUMMERS. 1971. Temperature effects on the developmental rate of squid (*Loligo pealei*) embryos. Biol. Bull. 141:561–567.

NAEF, A. 1928. Die Cephalopoden. Fauna Flora Golf Neapal 35(II):357 pp.

NIXON, M. & J. B. MESSENGER. 1977. The biology of cephalopods. Symposia of the Zoological Society of London, No. 38. Academic Press: London. 615 pp.

PACKARD, A. 1985. Sizes and distribution of chromatophores during post-embryonic development in cephalopods. Vie et Milieu 35(3/4):285–298.

ROPER, C. F. E., M. J. SWEENEY & C. E. NAUEN. 1984. Cephalopods of the world: an annotated and illustrated catalogue of species of interest to fisheries. FAO Fisheries Synopsis 3(125):277 pp.

SINGLEY, C. T. 1977. An analysis of gastrulation in *Loligo pealei.* Ph.D. Thesis, University of Hawaii, Honolulu.

SUMMERS, W. C. 1983. *Loligo pealei.* Pp. 115–142. *In:* P. R. Boyle (ed.), Cephalopod life cycles. Vol. I: Species accounts. Academic Press: London.

TANSEY, E. M. 1979. Neurotransmitters in the cephalopod brain. Comp. Biochem. Physiol. 64C:173–182.

THOMAS, H. J. 1973. Squid. Scottish Fisheries Bulletin 39: 35–39.

WORMS, J. 1983a. World fisheries for cephalopods: a synoptic overview. FAO Fisheries Technical Papers (231):1–20.

WORMS, J. 1983b. *Loligo vulgaris.* Pp. 143–157. *In:* P. R. Boyle (ed.), Cephalopod life cycles. Vol. I: Species account. Academic Press: London.

YANG, W. T., R. T. HANLON, R. F. HIXON & W. H. HULET. 1980. First success in rearing hatchlings of the squid *Loligo pealei* Lesueur, 1821. Malacol. Rev. 13:79–80.

YANG, W. T., R. F. HIXON, P. E. TURK, M. E. KREJCI, W. H. HULET & R. T. HANLON. 1986. Growth, behavior, and sexual maturation of the market squid, *Loligo opalescens,* cultured through the life cycle. Fish. Bull. 84(4):771–798.