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Authors: Shigeno, Shuichi, Kidokoro, H., Goto, T., Tsuchiya, K., and Segawa, Susumu

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Early Ontogeny of the Japanese Common Squid *Todarodes pacificus* (Cephalopoda, Ommastrephidae) with Special Reference to its Characteristic Morphology and Ecological Significance

Shuichi Shigeno[1], H. Kidokoro[2], T. Goto[2], K. Tsuchiya[3], and Susumu Segawa[3]*

[1]*Ushimado Marine Laboratory, Graduate School of Natural Science and Technology, Okayama University, Ushimado, Okayama 701-4303, Japan*
[2]*Japan Sea National Fisheries Research Institute, Niigata 951-8121, Japan*
[3]*Laboratory of Invertebrate Zoology, Tokyo University of Fisheries, Minato-Ku, Tokyo 108-0075, Japan*

ABSTRACT—Early ontogeny of the Japanese Common Squid *Todarodes pacificus* was described for artificially inseminated and collected specimens to present new criteria for developmental stages in relation to its ecological adaptation. For the purpose, details for formation of the following organs and tissues were observed with special attention: cilia on the integument, mouth part, shell sac and stellate ganglia, visceral mass, funnel-collar complex, statocysts, eye parts, and ventral photosensitive vesicles. At the embryonic stage (i.e., pre-hatching), various types of epidermal cilia that seem to work as the embryonic rotation were detected. At the early postembryonic stage (i.e., post-hatching), the epidermal lines were characteristically arranged at the scattered condition on arms, tentacles, head, and funnel. Novel strong muscle fibers were distinct in the base of tentacles and funnel retractor muscles at the early postembryonic stage, which is clearly related to the head withdrawal behavior of the paralarvae. The lip cilia and toothed beak developed at the early postembryonic stage, but disappeared later; these apparatus were considered to be related with a change of unique feeding mode in the paralarval life. Based on such morphological features, four distinct stages, namely, paralarval stage 1, 2, 3, and juvenile stage are proposed. The present observations are discussed in relation to survival strategy at early life of *T. pacificus* and they are compared with those in other cephalopods.

INTRODUCTION

Cephalopods develop without cataclysmal metamorphosis and they undergo meroblastic nonspiral cleavage, epibolic gastrulation, and direct development (Naef, 1928; Fioroni, 1978; Boletzky, 1989). The planktonic young are generally adult-like, whereas certain species meet morphological and ecological changes in the early life (Boletzky, 1974; Nesis, 1980; Fioroni, 1982), thus the term “paralarva” was introduced for cephalopod “larva” (Young and Harman, 1988). Early ontogeny in cephalopods is mainly studied on neritic groups, e.g., myopsids and sepioids (Boletzky, 1974, 1987, 1989 for reviews). Our knowledge is still limited on pelagic or sub-pelagic ommastrephids that have smaller eggs in size and morphologically specific paralarval form (Watanabe *et al.*, 1996).

The Japanese Common Squid, *Todarodes pacificus* Steenstrup, 1880 (Cephalopoda, Ommastrephidae) living in mainly offshore water is known as one of the most commercially important cephalopod in Japan (Okutani, 1983). However, the early life of *T. pacificus* has not yet been unveiled mostly due to the difficulty in obtaining spawned eggs and paralarvae from ocean. These situations leaded some pioneer works on early ontogeny of this species, in which the embryonic development were described for the specimens obtained by preliminary designed artificial insemination (Soeda, 1952, 1954; Hayashi 1960). Gross observations on the behavior and external morphology of *T. pacificus* embryo and paralarva were done based on captive specimens (Hamabe, 1961, 1962). Further studies have been made on the early ontogeny of *T. pacificus* with special reference to the paralarval

* Corresponding author: Tel. 03-5463-0525;
FAX. 03-5463-0687.
E-mail: segawa@tokyo-u-fish.ac.jp,

morphology for taxonomic and ecological aspects in naturally collected specimens (Okutani, 1965; 1983; 1987 for reviews). Recent detailed analysis on the embryonic development has been made possible by technical establishment of the artificial insemination in *T. pacificus* (Ikeda *et al.*, 1993), and the embryonic and early postembryonic stages were completely described (Watanabe *et al.*, 1996). These results on *T. pacificus* would be applicable and comparable to the information of other ommastrephids (e.g., *Illex* spp. Naef, 1923, 1928; Boletzky *et al.*, 1973; O'Dor *et al.*, 1982, 1985, 1986; Vidal, 1994; Sakai and Brunetti, 1997; Vidal and Haimovici, 1998; *Sthenoteuthis* Sakurai *et al.* 1995). Contrary to many previous works on description for ontogeny of ommastrephids, there is a few information on histological and ultrastructural details for insights into the functional morphology and its ecological significance.

Following characteristic features were recognized for ommastrephids early ontogeny based on ecological and morphological studies: numerous numbers of small sized eggs at spawning, morphological unique style of paralarva called as rynchoteuthion which is characterized by fusion of paired tentacles into a proboscis (Okutani 1987, Boletzky, 1993 for reviews). Related to the small egg size, organogenesis of *T. pacificus* undergoes heterochronic shifts compared with those in myopsids (e.g., *Loligo*), which is characterized by delay of the development on various organs such as gills, digestive organs, statocysts, and absence of the large outer yolk sac. Early ontogeny of this group is also characterized by large egg mass consisted of loose gelatinous substances (Hamabe, 1962; Bower and Sakurai, 1996). These features are also shared in mesopelagic squids (Young and Harman, 1985; Young *et al.*, 1985; Hayashi, 1989; Arnold and O'Dor, 1990; Watanabe, 1997) and some are comparable to epipelagic octopods (Naef, 1928; Sacarrão, 1949), which have been explained as an adaptation to the pelagic life (Arnold and O'Dor, 1990; Watanabe *et al.*, 1996)

The purpose of the study is to observe morphological and histological aspects of early stages of *T. pacificus*, by which new criteria for the developmental stage is proposed and its ecological adaptation is discussed. For that purpose, in addition to general morphological information of embryo and paralarva, the present study focused on particular ultrastructure of organs and tissues including cilia on integument, epidermal lines, shell sac, sensory organs, toothed beak, and

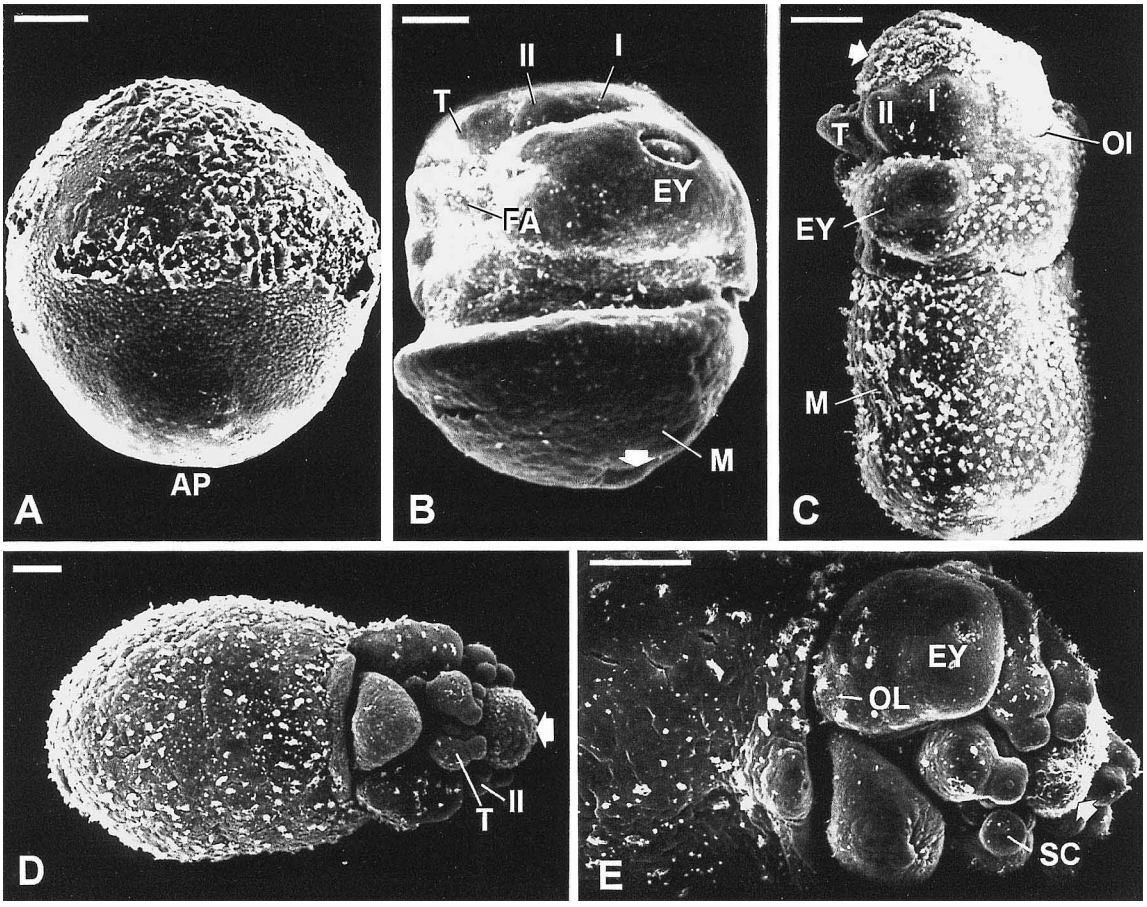


Fig. 1. Scanning electron micrographs of the surface structure of embryos and a newly hatched paralarva of *Todarodes pacificus*. (A) St 12, the half epibolic growth. (B) St 18, the oblique ventral view with the primordial funnel. The arrow indicates closure of the shell gland. (C) St 22, the dorsolateral view with the oral ingrowth. The arrow indicates the outer yolk sac. (D) St 25, the ventral view. The arrow indicates the outer yolk sac. (E) St 26, the oblique ventral view of the head of hatchling. The arrow indicates the outer yolk sac. AP, animal pole; EY, eye vesicle; FA, anterior funnel fold; M, mantle; OI, oral ingrowth; OL, olfactory organ; I-II, arm I-II; SC, sucker; T, tentacle; Scale bars 0.1mm.

funnel retractor muscles.

MATERIALS AND METHODS

The embryos, paralarvae, and juveniles were obtained from artificial insemination on board or field collection at the Sea of Japan. Developmental stages on embryo and early paralarva of *T. pacificus* followed the criteria of Watanabe *et al.* (1996). Stages during the postembryonic period were established according to the present observations. Dorsal mantle length (ML) was measured in post-fixed specimens. The fixed specimens usually exhibit artificial shrinkage about 80%, e.g., 1.0mm ML (mantle length) of newly hatched paralarva became 0.8mm ML after fixation.

Artificial insemination and cultivation

Experiments were performed on July 1997 during a cruise of the R/V Choukai-Maru (452.0t) of Yamagata Prefectural Kamo Fisheries Senior High School. Live animals were captured by squid jigging and matured females were selected based on the existence of ripe ova in oviducts and numerous spermatangia on the seminal receptacle of the buccal membrane. Artificial insemination was applied to obtain the fertilized eggs according to the method described by Ikeda *et al.* (1993) and Sakurai *et al.* (1995, 1996). Ova and sperm masses were respectively collected from oviduct and seminal receptacle of mature female. After the sperm-seawater mixture was added to the ova in the petri dish, fresh dissected oviducal gland pieces suspended in seawater were mixed with the fertilized eggs, which induce formation of perivitelline space of fertilized egg. The eggs were incubated in filter-sterilized and aerated seawater at ca. 20.5°C. Embryos and hatchlings were staged under a stereomicroscope, then they were fixed, and stored in 70% ethanol at 4°C. After crews, some of the embryos were transported in a cool box (for ca. 30 minutes) and cultivated in an incubator (dark room, 20.5°C) without being fed up to stage 31 at the Japan Sea National Fisheries Research Institute.

Field collection

The postembryonic specimens except for cultivated paralarvae and juveniles were collected at the Sea of Japan during a cruise of the T/V Mizunagi (148.0t) of Kyoto Prefectural Marine Senior High School on October 1995 and 1996. Samplings were made with oblique haul from a depth of about 75m by a cylinder-cone ring net or long-NORPAC net. Juveniles of 38mm and 45mm in ML were collected with a set net in the coast of the Sea of Japan at Kunda-Oda, Kyoto Prefecture on February 1997. Some juveniles (ca. 28mm in ML) were dip netted on board of the R/V Choukai-Maru (see above).

Histological observation

For histological observation, artificially inseminated specimens were fixed with Bouin's solution (12–24 hrs at 4°C) and stored in 70% ethanol (several months at 4°C). The field-collected specimens were fixed in 5–10% formalin seawater (1day at room temperature) and

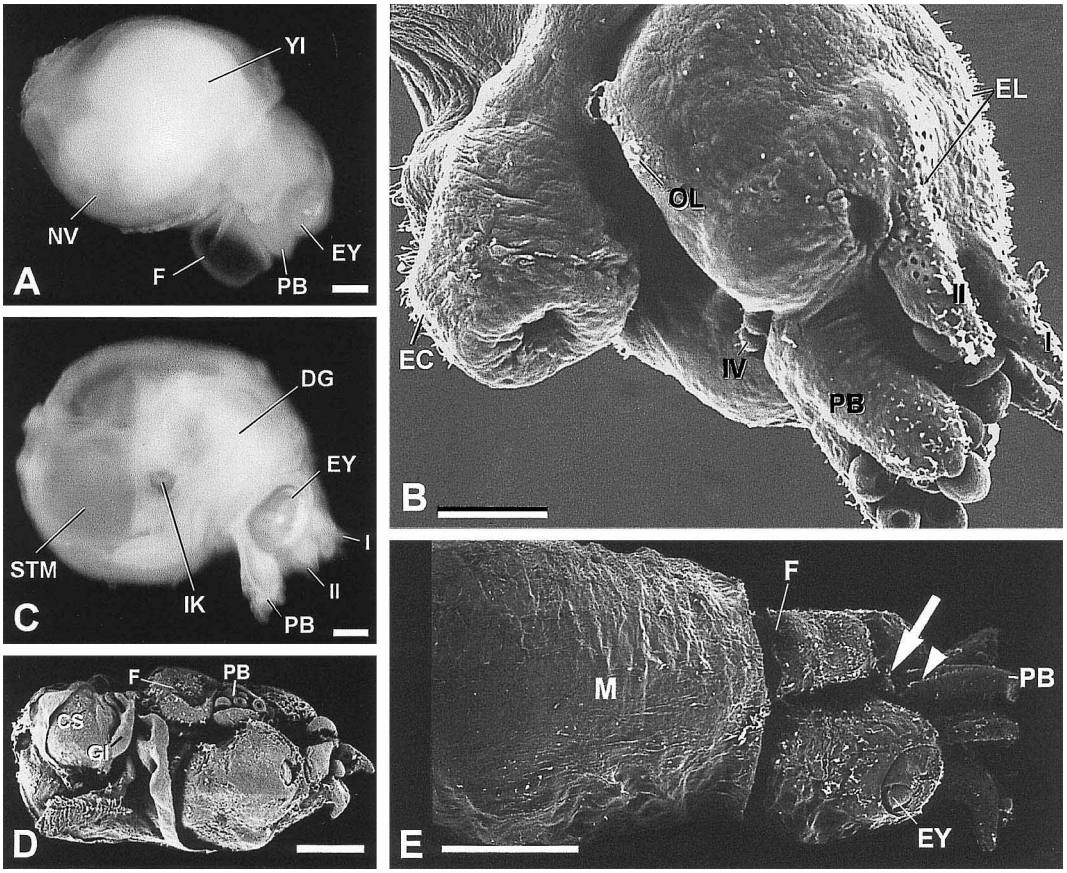


Fig. 2. Paralarvae of *T. pacificus*. (A) Paralarval stage 1, lateral view (field collected specimen). (B) Paralarval stage 1, lateral view of the head (SEM). (C) Paralarval stage 2, lateral view (field collected specimen). (D) Paralarval stage 2 (SEM, ML 1.0mm, oblique ventral view) without the mantle. (E) Paralarval stage 3 (SEM, ML 3mm, oblique ventral view). The large arrow indicates small buds of arm IV at the base of fused tentacle. The fused tentacle begins to separate at the base (small arrowhead). CS, coelom sac; DG, digestive gland; EC, cilia of funnel epidermal line; EL, epidermal line; EY, eye; F, funnel; GI, gill; I-IV, arm I-IV; IK, ink sac; OL, olfactory organ; PB, proboscis; M, mantle; NV, nascent visceral mass; STM, stomach; YI, inner yolk. Scale bars, 0.1mm (A, B, C), 0.5mm (D), 1mm (E).

stored 5% phosphate buffered formalin (several years at room temperature). Fixed samples were dehydrated by graded ethanol and embedded in Paraplast. Serial sections were made with a rotary microtome (thickness, 3–5 μm for embryos and early paralarvae, 10–15 μm for large postembryonic specimens), rehydrated, and stained with Mayer's hematoxylin and eosin (HE), or Masson trichrome (Masson) by which fibrous tissues are prominent. The Cajal's silver staining (Cajal) was applied according to the method of Stephens (1971). Cajal's technique is usually useful for the neural anatomical study, and is also available for the purpose of general histology. To observe histological details, the semithin sections (1–2 μm) were made with Spurr's resin and an ultramicrotome; they were stained with toluisin blue (TB).

Scanning electron microscopy (SEM)

Specimens were fixed with Bouin's solution (12–24 hr at room temperature) or 2.5% glutaraldehyde/seawater (1 hr at 4°C), and washed and stored in 70% ethanol. Some specimens were imbedded in paraplast and dissected with microtome as stated above. The dissected wholemount specimens were deparaffinized in xylen and transferred to graded ethanol and finally stored in 70% ethanol. The stored specimens in 70% ethanol were dehydrated via graded series of ethanol, immersed in t-butyl alcohol (2-methyl 2- propanol), and dried with a freeze dryer (JEOL, JFD-300). They are coated with gold by a coater (JEOL, JFC-1100) and viewed with a SEM (JEOL, JSM-100).

RESULTS

Characterization of the developmental stages

***Embryonic stage* (Fig. 1; up to St 26):** After cleavage and blastulation occurred at the animal pole side, the epibolic gastrulation progresses (Fig. 1A). Organogenesis begins in the late epibolic period (from St 16, Watanabe *et al.*, 1996). Placodal thickenings of the arm crown arise as three buds of arm I, II, and tentacle (Fig. 1B). Eye, funnel fold, and mantle are also visible as placodal thickenings. The sucker first appears on tentacle (St 22: Fig. 1C). Overall shape of the embryo elongates antero-posteriory. A small swelling of outer yolk sac is situated at the anterior periphery of embryos. At later stages, the extent of outer yolk sac is limited within the area of arm crown (Fig. 1D). Oral ingression is observed at the dorsal surface. In later embryonic stage, the outer yolk

Table 1. List ot *Todarodes pacificus* used for the present histological observations. STAGE, ontogentetic stage proposed in the present study. CJ, block silver method of Cajal; ML, dorsal mantle length; HE, hematoxylin and eosin; INY, presence of inner yolk (Y); MS, Masson trichrom: pre, fixed by head withdrawal situation (as "prerhynchoteuthis", see Okutani, 1965); PSV, ventral photosensitive vesicles; SFM, strong muscle fibers in the funnel retractor muscles; STAIN, staining methods.

STAGE	ML (mm)	STAIN	FORM	INY	NOTABLE CHARACTERS
PARALARVA 1	0.60	HE		Y	St 28. No Ink. SFM and Lip cilla visible.
	0.60	HE		Y	St 31. Toothed beak visible.
	0.60	HE		Y	St 31. Ink sac fills with ink.
	0.60	HE	pre	Y	St 33. 1 leaflets of gills Primary lid complete. Outer lens begin.
	0.80	HE	pre	Y	St 33.
PARALARVA 2	0.60	HE		Y	2 leaflets of gills.
	0.70	HE			
	0.79	HE			
	0.80	HE			
	0.80	MS	pre		
	0.90	HE			
	0.92	HE	pre		
	0.94	HE			
	0.96	HE	pre		3 leaflets of gills.
	1.00	HE	pre		
	1.04	HE			Tentacle length 0.20mm.
	1.06	HE	pre		
	1.10	HE	pre		
	1.10	MS			4 leaflets of gills.
	1.60	HE	pre		
	1.60	MS	pre		6 leaflets of gills.
PARALARVA 3	2.40	CJ			No. lip cilia. Outer lip begins ot be vent into folds. Arm III visible.
	2.40	CJ			
	2.40	CJ			
	2.50	HE			6 leaflets of gills. Lobulated pancreas. Toothed beak visible. PSV visible.
	2.90	HE			No toothed beak. Fused tentacle begins to separate.
	3.90	HE			12 leaflets of gills.
	5.50	MS			
	7.10	HE			
JUVENILE	16.00	CJ			Separation of fused tentacle. No lip cilla.
	25.00	CJ			Slender cone-shaped mantle. Triangle fins.
	28.00	CJ			
	38.00	MS			
	45.00	CJ			

sac reduces in size and three paired arms and tentacles begin to elongate (Fig. 1D). In the hatching stage (St 26), a small outer yolk sac still remains (Fig. 1E). Suckers exist on arms and tentacles with nascent acetabulums and inner rings. Many cilia are observed on the embryonic integument including outer yolk sac at the later stage.

Paralarval stage 1 **(Fig. 2A, B; St 27-34):** Presence of inner yolk sac is visible (Fig. 2A). Many undifferentiated organs such as balloon-shaped mantle, relatively large funnel, weak arms (I, II), small round fins, and nascent visceral mass are observed at the paralarval stage 1. A pair of arm IV begin to appear as swollen buds at the ventral base of proboscis, but arm III is not distinguished at the area between arm II and tentacle (Fig. 2B). Secondary eyelids cover the eye vesicles and complete the oegopsid typed eye. A few suckers are present on arm I and II. The proboscis begins to fuse at the base of tentacles.

Paralarval stage 2 **(Fig. 2C):** Field collected specimens (0.6mm - 1.6mm ML, n=16) were examined for the paralarval stage 2 (Table 1). Outer feature at the paralarval stage 2 is similar to those of the previous stage; relatively large funnel, balloon-shaped mantle, nascent arms, small eyes, and round-shaped small fins. However the inner yolk is completely absorbed and the large developed visceral mass is clearly detected on whole mount specimens of the paralarval stage 2 (Fig. 2C). The most paralarvae have a large stomach filled with particles. The arm crown consists of arm I, II, proboscis (tentacle), and arm IV. A pair of gills are considerably nascent with countable numbers of leaflets (Fig. 2D). Withdrawal of the head into the mantle cavity (Okiyama, 1965) is observed in the majority of fixed specimens.

Paralarval stage 3 **(Fig. 2E):** Field collected specimens (2.4mm–7.1mm ML, n=8) were examined (Table 1). Presence of arm III is a major criterion for the paralarval stage 3. On the ventral side of proboscis, a gulf is observed (Fig. 2E). This indicates that proboscis begins to separate at the base, forming paired tentacles. Compared to the paralarval stage 2 (Fig. 3A), the arms and tentacles somewhat elongate (Fig. 3B). The mantle begins to elongate longitudinally, whereas fins are still small and round in shape. All members of arms are distinguished. Development of arm IV varies by individual from the bud situation (3.0mm ML, Fig. 2E) to well developed state (2.4mm ML, Fig. 3B). Funnel becomes proportionally small (10% of ML) compared with that in the previous stage (33%): The head withdrawal into mantle cavity was not observed in fixed specimens of this stage. Gills are laminated with many leaflets, which increase from six to twelve numbers per a gill.

Juvenile stage **(Fig. 3C):** Field collected specimens (16mm - 45mm ML, n=5) were examined. Proboscis is completely separated into tentacles. All the arms are similar in length. The number of leaflets of gills is twelve or more (Table 1). The growth of gills is a characteristic feature to show the development of circulatory system and metabolism in this stage. More longitudinal elongation of the mantle is evident and finally, the shape becomes slender cone-shape (Fig. 3C). Fin becomes to triangle-shape. Compared to paralarval stage 2 and 3, eyes grow largely, but the supraesophageal mass (a part of the brain) and optic lobes are relatively similar in size (Fig. 3A, C).

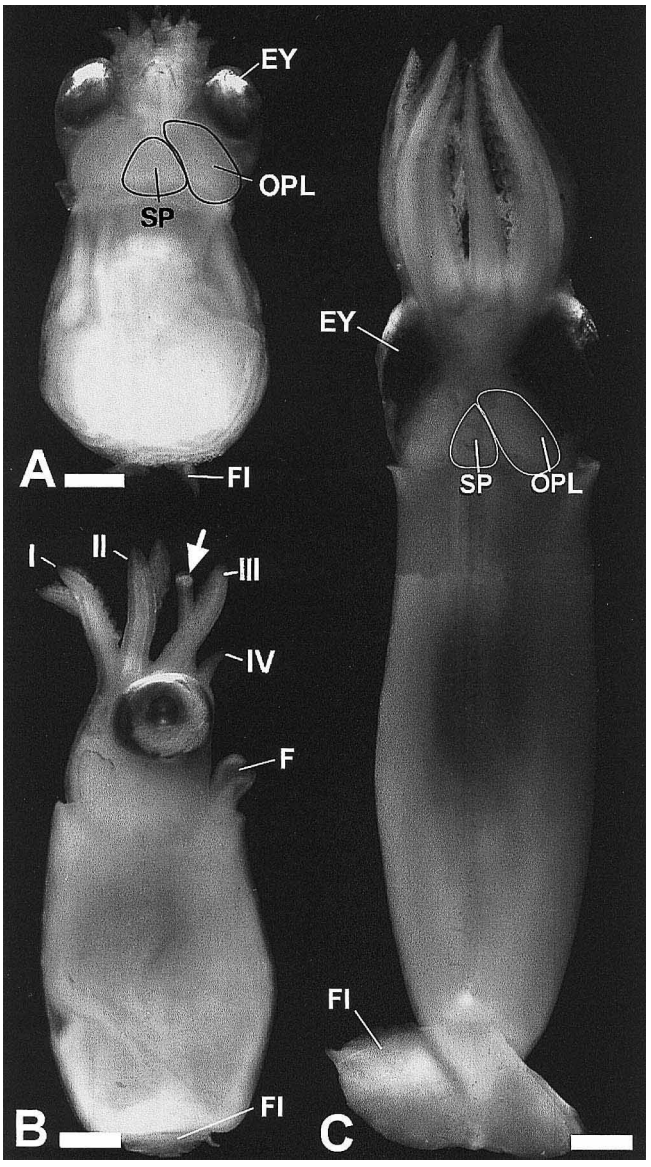


Fig. 3. Field collected paralarvae and juvenile of *T. pacificus*, showing the external form including eye and brain. (A) Paralarval stage 2 (ML 1.6mm), (B) Paralarval stage 3 (ML 2.4mm). The arrow indicates fused tentacle (proboscis). (C) Juvenile stage (ML 16mm). EY, eye; F, funnel; FI, fin; OPL, optic lobe; SP, supraesophageal mass of the brain; I-IV, arm I-IV; Scale bar, 0.32mm (A), 0.4mm (B), 0.8mm (C).

Formation of selected organs and tissues

Cilia on the integument**:** Ciliary structures were observed with histological sections and SEM. On the embryonic integument, seven types of cilia are described (Fig. 4A). Some types of cilia degenerate at early of paralarval stage 1.

(1) Scatter-type cilia: This type of cilia is conspicuous, which is only observable on the surface of outer yolk sac (Fig. 4A). The cilia appear earlier than remaining types of cilia (St 18, Fig. 4B). The cilia elongate at late of this stage (Fig. 4C).

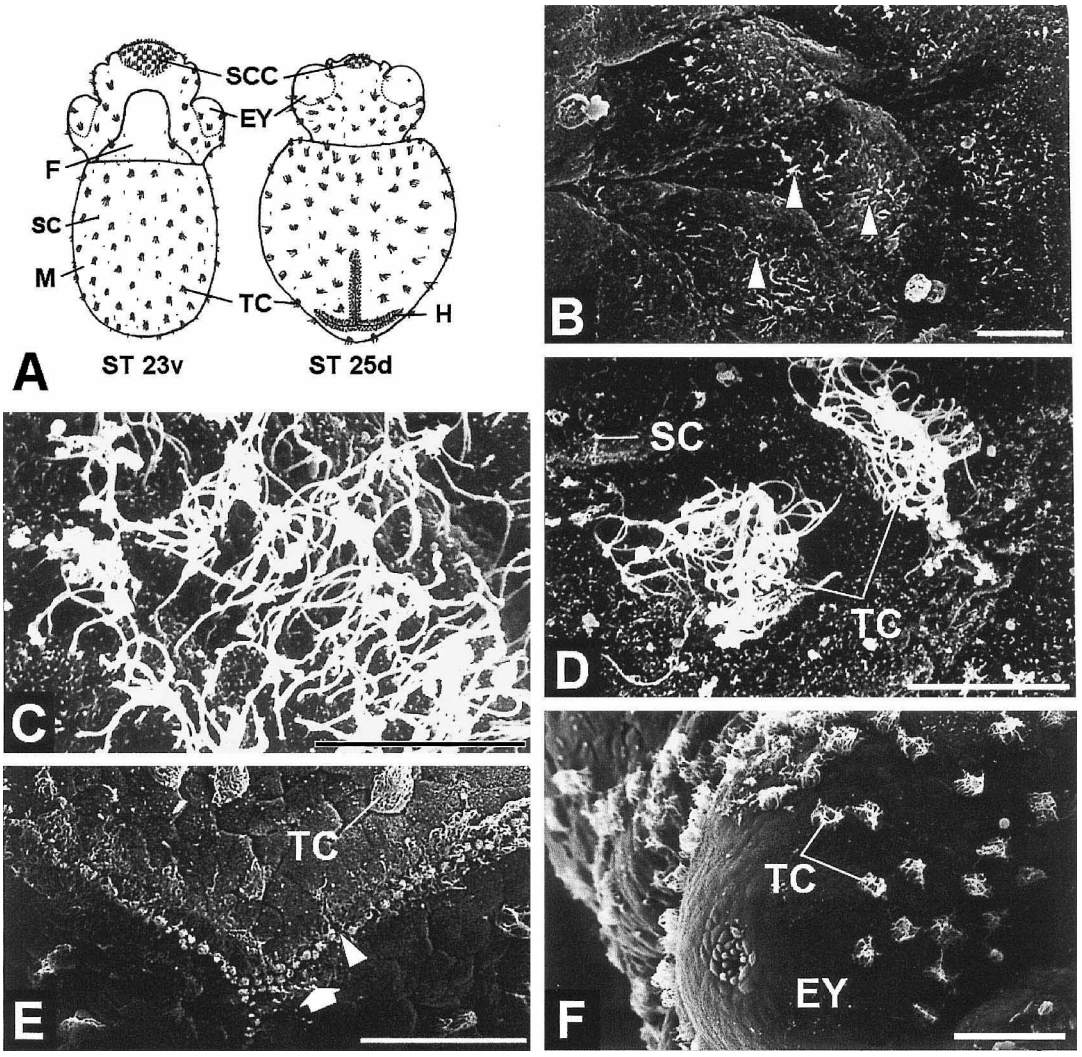


Fig. 4. Cilia on the embryonic integument of *T. pacificus*, SEM. (A) Schematic drawings of embryos and distributed cilia, the ventral (St 23) and dorsal (St 25) view. The cilia are not corresponding to actual numbers. (B) Scatter-type cilia (arrowheads) on the outer yolk sac, St 18. (C) Scatter-type cilia on the outer yolk sac, St 22. (D) Tuft- and single-type cilia on the mantle, St 22. (E) T-shaped Hoyle's organ and support-type cilia (arrow) at the dorsal mantle, St 25. The arrowhead indicates alpha-cell of Hoyle's organ. (F) Eye vesicle and tuft-typed cilia, St 25. (C) Scale bar, 0.01mm (B, C, D), 0.05mm (E, F). EY, eye; F, funnel; H, Hoyle's organ; M, mantle; SC, single-type cilia, SCC, scatter-type cilia on the outer yolk sac; TC, tuft-type cilia.

Exact boundary between the outer yolk sac and embryonic body is detected by existence of these scattered cilia on the surface of yolk sac.

(2) Single-type cilia: A few cilia are dispersively distributed on the integument of mantle, head, and arms. This type of cilia is considered as sensory organ (Sundermann-Meister, 1978) and clearly different from tuft-type cilia because of its short length (Fig. 4A, D).

(3) Tuft-type cilia: The cilia exist on the embryo proper, which have a stir function of the perivitelline fluid with scatter-type cilia (Arnold and Williams-Arnold, 1980). The cilia distribute as many patches (Fig. 4D, E), which were never observed at a part of eye capsules, suckers, dorsal areas of arms, and ventral sides of the funnel (Fig. 4F; see Fig. 4A for the overall pattern). Histological observation reveals that these cilia arise from a cell proper (Fig. 5A).

(4) Support-type cilia: The cilia are visible around the Hoyle's organ (alpha- and delta-cells that have an adhesion function to chorion at the hatching moment and secretionaly function of enzyme, respectively; Arnold and Singley, 1989; Fig. 4E). This type of cilia is clearly different from tuft-type cilia, showing a comparatively uniform distribution. A histological section shows that these ciliary cells are not distinguished form cells of Hoyle's organ at the early embryonic stage (Fig. 5B). At a pre-hatching stage (St 25), The ciliary cells are clear, which are situated at the distal side of Hoyle's organ (Fig. 5C).

(5) Cilia on the olfactory organs: The chemoreceptive organs are situated at the ventral head of embryos and paralarvae (Fig. 6A). It is difficult to distinguish the cilia at the embryonic stage, but a few cilia are clearly observable at the paralarval stage (cf. Fig. 1E and 2B).

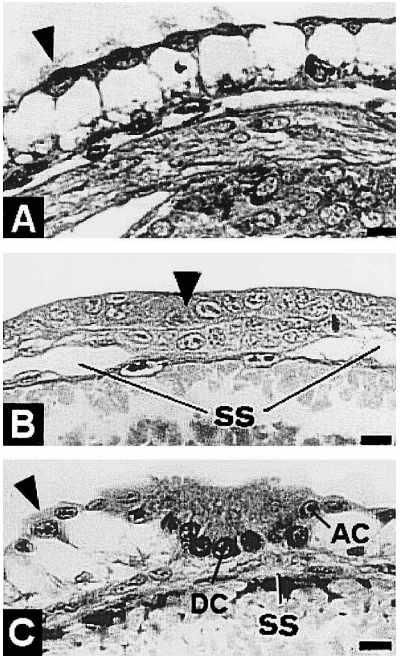


Fig. 5. Histological sections of *T. pacificus*. (A) Tuft-type cilia (arrowhead) of the mantle (St 26, TB), (B) Developing Hoyle's organ (arrowhead, St 19, Masson). (C) Hoyle's organ at pre-hatching stage (St 25, HE). Support-type cilia are indicated with an arrowhead. SS, shell sac; DC, delta-cell; AC, alpha-cell. Scale bars, 0.01mm.

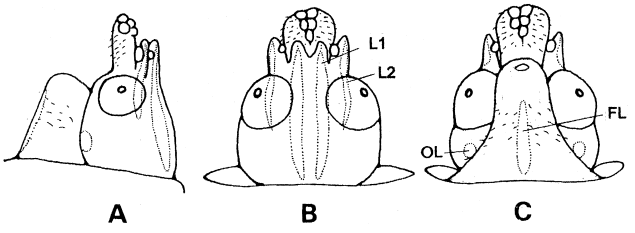


Fig. 6. Pattern of epidermal cilia of the head in *T. pacificus*, the lateral (A), dorsal (B), and ventral (C) view. Epidermal lines are presented as dotted area exhibiting the ciliary band situation. L1, epidermal line 1 (the dorsal line); L2, epidermal line 2 (dorso-lateral line); FL, epidermal line on the ventral side of funnel. OL, olfactory organ.

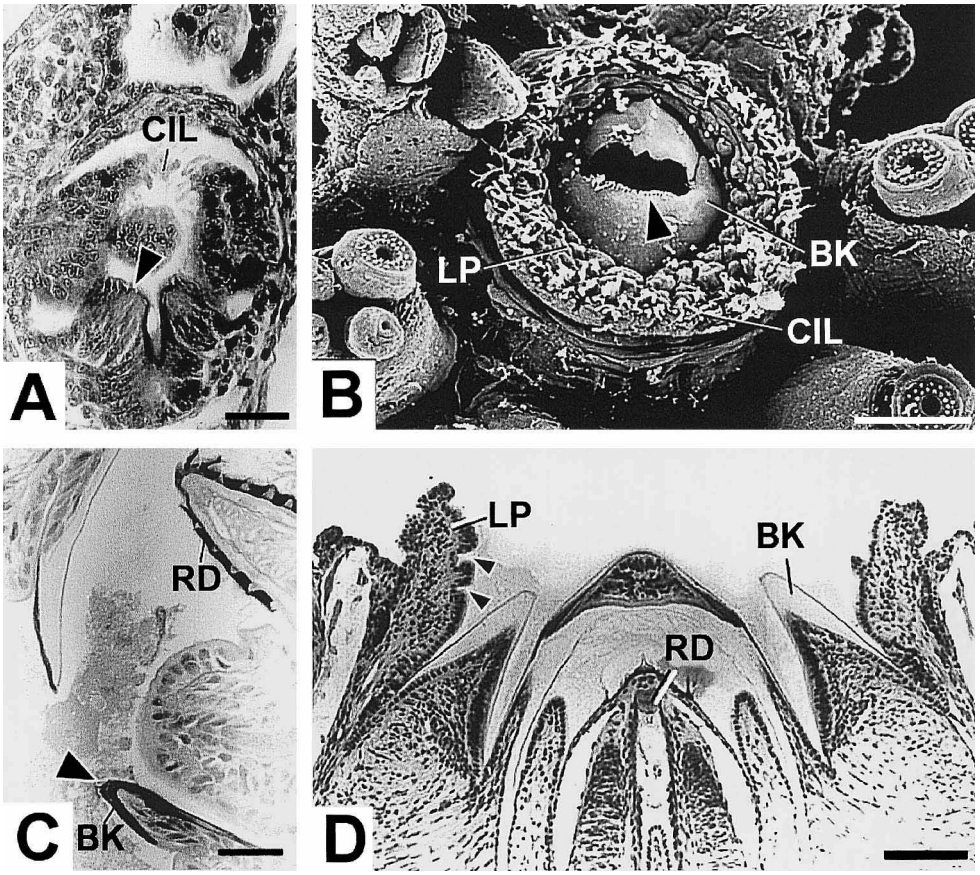


Fig. 7. The mouth part of *T. pacificus*. (A) A transverse section of lip cilia and toothed beak (arrowhead) of paralarval stage 1 (St 30, Masson). (B) Lip cilia and toothed beak (arrowhead) of paralarval stage 1, SEM (ML, 1.0mm). (C) A sagittal section of the buccal mass and toothed beak (arrowhead) of paralarval stage 2 (ML 1.0mm, HE). (D) Apical region of the buccal mass to show the folded lip of paralarval stage 3 (ML 5mm, horizontal section, HE). BK, beak; CIL, lip cilia; LP, lip; RD, radula. Scale bars, 0.05mm (A, B, C), 0.2mm (D).

(6) Epidermal lines: Massive cilia of epidermal lines which is lateral line analogue of fish (see Budelmann, 1994) are situated on arms, tentacles, head, and ventral side of the funnel (Fig. 6A-C). Cilia of epidermal lines in banding pattern occupy a large area of arms and the head. Dorsal lines (L1) and dorsolateral lines (L2) are running from the dorsal periphery of arms I, and II to the head, respectively. Arrangement of ciliary lines shows multiple rows (from 2 to 5 rows; see Fig. 2B). There is not evident cilial line on tentacles (proboscis), but scattered cilia appear randomly on the dorsal and dorsolateral surfaces of the proboscis.

(7) Lip cilia: The cilia distributed on the outer lip are first observed after the stage of complete digestion of outer yolk sac (paralarval stage 1; Fig. 7A). The cilia are present up to the specimen of 1.6mm ML at the end of paralarval stage 2 (Fig. 7B). At the paralarval stage 3, the outer lip of the paralarvae begins to bent into folds and the lip cilia are not detected (Fig. 7D).

The mouth part: Oral ingression appears on the dorsal head part in St 17, forming future buccal mass (Watanabe *et al.*, 1996). Ingression of posterior salivary gland arises in St 21, and a duct of salivary gland are divided into a pair of salivary sacs at the posterior region of buccal mass. At paralarval stage 1 and 2, the lower beak is fully toothed and every tooth is nearly the same in size and regularly arranged (Fig. 7A-C). The upper beak divides into two at the periphery without teeth. This feature of the upper beak is considered as a developing situation of the beak (Boletzky, 1971). At paralarval stage 3, teeth on the lower beak were still present in the specimen of 2.5mm ML, but not present in the specimen of 2.9mm ML. At the juvenile stage, beaks develop strongly and teeth on the lower beak completely disappear. In the buccal mass, radula, beak, and supported muscles are strongly developed.

The shell sac and stellate ganglia: Cellular assemblage of shell gland appears in St 16 (Watanabe *et al.*, 1996). The gland is detected in the animal pole at previous cleavage location. Subsequently, the shell sac begins to be covered by circumference of ecto- and mesoderm in St 18. In St 18, mesodermal cells that form future mantle muscles begin to arise from the periphery of embryos. The mesodermal cells prolif-

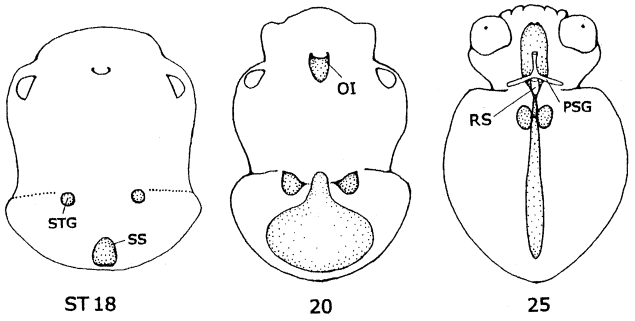


Fig. 8. Early development of stellate ganglia, shell sac, oral ingrowth, and posterior salivary glands in *T. pacificus*, the schematic figures (dorsal view). Numbers indicate the developmental stages. OI, oral ingrowth; PSG, posterior salivary gland; RS, radular sac; SS, shell sac; STG, stellate ganglion.

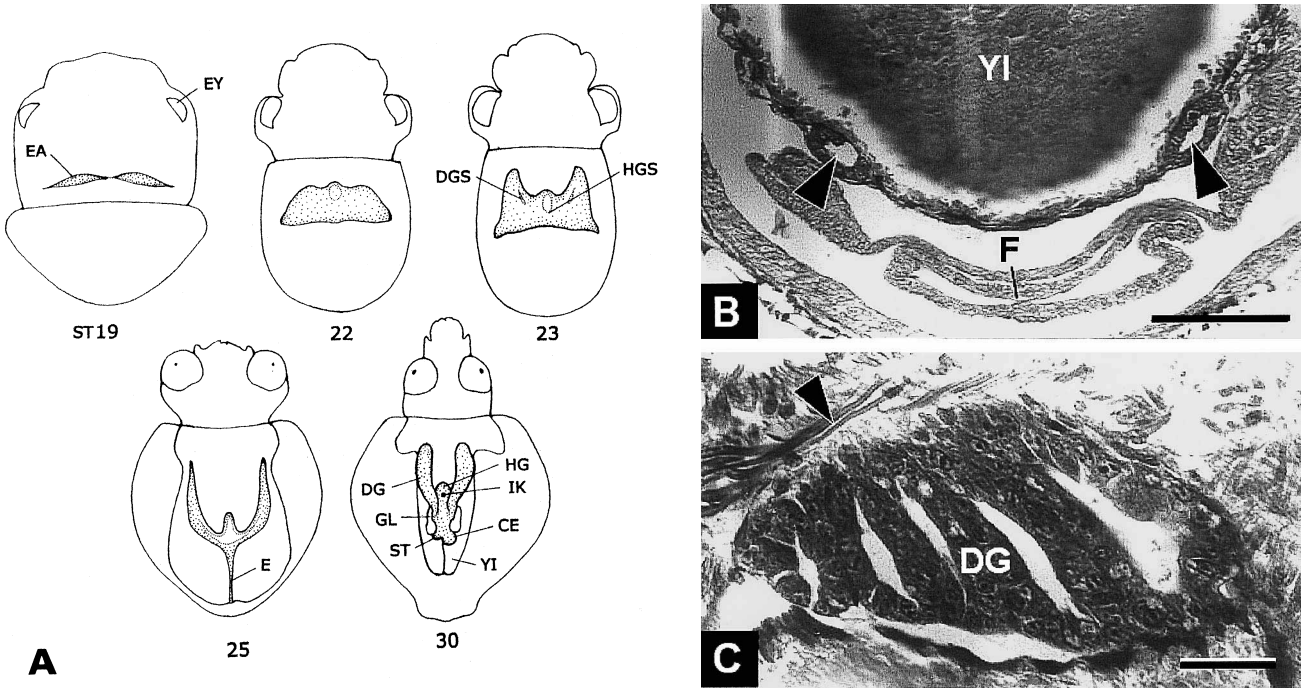
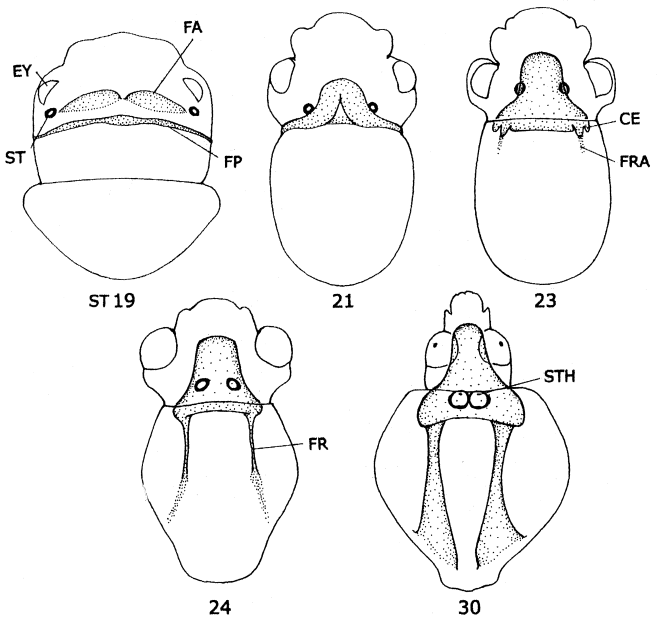


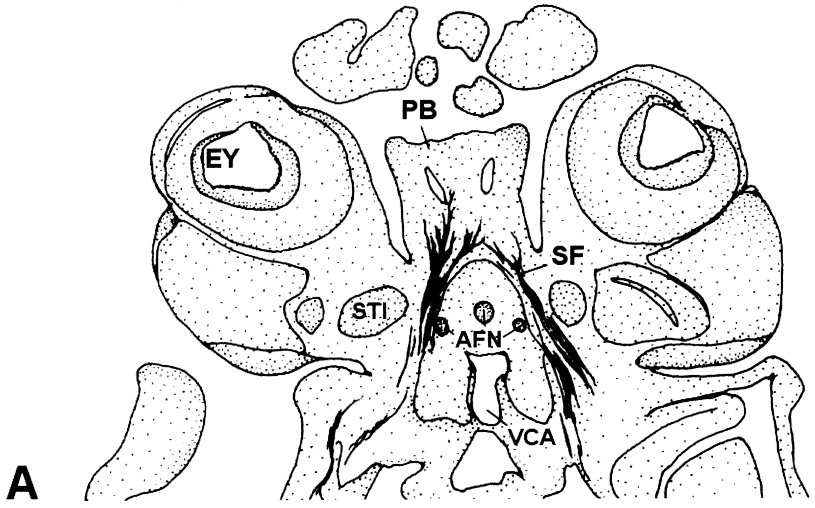
Fig. 9. Development of the digestive organ in *T. pacificus*. (A) Schematic figures (ventral view). Numbers indicate the developmental stages. (B) Internal space of nascent digestive glands (arrowheads, St 28; transverse section, HE). (C) Lobulated digestive glands and strong muscle fibers (arrowhead, St 31; horizontal section, Masson). DG, digestive gland; DGS, internal space of digestive gland; CE, caecum; E, esophagus; EA, endodermal cellular anlage; EY, eye; F, funnel; GL, gill; HG, hindgut; HGS, internal space of hindgut; IK, ink sac; ST, stomach; YI, inner yolk. Scale bars, 0.2mm (B, C).



erate to the posterior direction. Shell sac that is oval shape in St 18, elongates dorsally, and a projection comes to anterior direction from St 20 (Fig. 8). Finally, the shape of shell sac becomes typical gladius-like in St 25. The mantle periphery elongates anteriory, forming an umbrella shaped mantle cavity. The stellate ganglia that are major centers of mantle innervation are formed at the anterior periphery in St 18, and these are finally located at the anterior both sides of the slender shell sac (Fig. 8).

The visceral mass: At the embryonic stage, visceral mass consists of various primordial organs, such as endodermal digestive tracts of midgut and hindgut, peripheral gan-

Fig. 10. Schematic figures of the development of funnel, funnel retractor muscles, and statocysts, (ventral view) of *T. pacificus*. Numbers indicate the developmental stages. CE, edge of collar; EY, eye; FA, anterior funnel fold; FP, posterior funnel fold; FR, funnel retractor muscle; FRA, cellular anlage of funnel retractor muscle; ST, statocyst; STH, statolith.



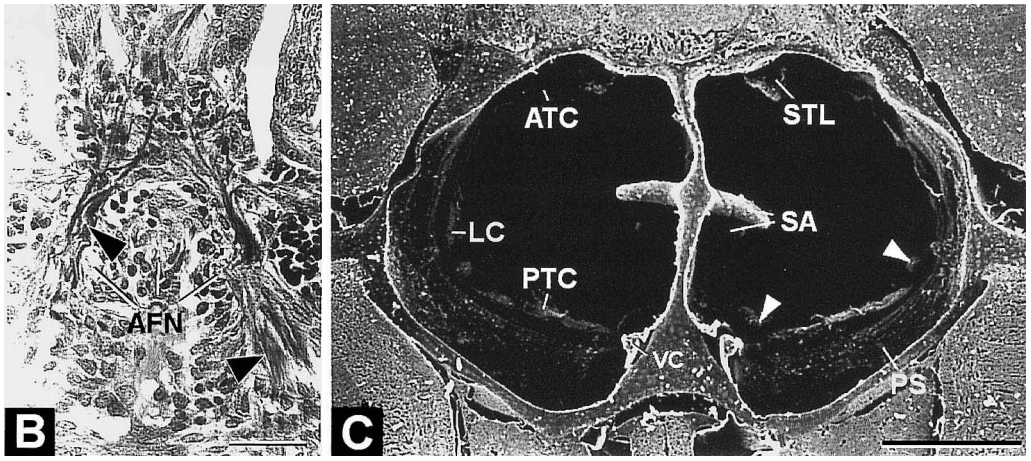


Fig. 11. (A) Semi-schematic drawing of a horizontal section of the head, showing the strong muscle fibers situated at the base of proboscis (St 29, Masson). (B) A horizontal section of strong muscle fibers (arrowheads) (St 29, Masson). (C) Statocysts, SEM (Juvenile stage, ML 38mm). The arrowheads indicate the projected hamuli. AFN, anterior funnel nerve; ATC, anterior transverse crista; EY, eye; LC, longitudinal crista; PB, proboscis; PS, posterior sac; PTC, posterior transverse crista; SA, straight anticristae; SF, strong fiber; STH, statolith; STI, subpedunculate tissue; VC, vertical crista; VCA, vena cava. Scale bars, 0.03mm (B), 0.5mm (C).

glia, mesodermal muscles, ink sac, circulatory and coelomic organs, gills, and reproductive organs (Marthy, 1968). These primordial organs are distinguished as two swellings on the ventral side in St 19 (Fig. 9A). From St 20, the visceral complex (mesendodermal cellular mass) is observed as three swellings; namely, a central swelling of hindgut and swellings on both sides of mainly nascent digestive glands and pancreatic appendages. The visceral primordium on the ventral side is concealed by the enlargement of mantle in St 22 (Fig. 9A). Rather restricted vena cava penetrates the boundary of these swellings in St 21. Inner spaces in primordial digestive glands first appear in the embryos of St 23 (Fig. 9A). The small spaces of the digestive organs project to periphery, and connections between digestive glands and hindgut are established. At paralarval stage 1, the inner yolk remains throughout the paralarval stage. Digestive glands are observed as a pair of anlagen with small inner space (St 28, Fig. 9B), and they begin to lobulate during the period of paralarval stage 1 (St 31, Fig. 9C). Pancreatic appendages are not yet fully differentiated at the paralarval stage 1, but these are clearly lobulated at the specimen of paralarval stage 2 (2.5mm ML, Table 1).

The funnel-collar complex: The funnel is composed of paired anterior funnel folds that develop to a future siphon, paired posterior funnel folds (collar), and funnel retractor muscles. The funnel occupies a large part of the embryonic body during the embryonic stage (Watanabe *et al.*, 1996). Right and left anterior funnel folds begin to fuse from anterior areas in St 21. In St 23, funnel retractor muscles arise from the ventral area of posterior funnel folds (Fig. 10). The funnel retractor muscles are elongating posteriory to develop along the surface of the ectodermal membrane of inner yolk sac, and finally these muscles connect in St 24 with posterior parts of mantle muscles (fin pouch) proximal to fin anlagen. At paralarval stage 1, strong specific muscle fibers are clearly detected in the funnel retractor muscles. These fibers, which are distinct from surrounding arm muscles and intensely stained by ponceau-xylidin of the Masson staining, are running from proboscis to the base of fins (Fig. 11A, B).

Statocysts: The organ is known as gravity and angular acceralation receptor systems (Budelmann, 1994) are situated at the ventral head region. At the embryonic stage, they primary originate as ectodermal placodes in proximal regions of anterior funnel folds in St 17 (similar feature is observed in St 19; see Fig. 10). The ectodermal placodes come to vent and to form sacs in St 20, and the duct of Kölliker that are connected with lateral part of statocyst (Stelzner *et al.*, 1997) have openings externally. The oval statocysts enter into direction of midline behind the fused anterior funnel folds in St 23 (Fig. 6). Both statocysts begin to contact each other in St 25. Vena cava flows into the ventral area of statocysts.

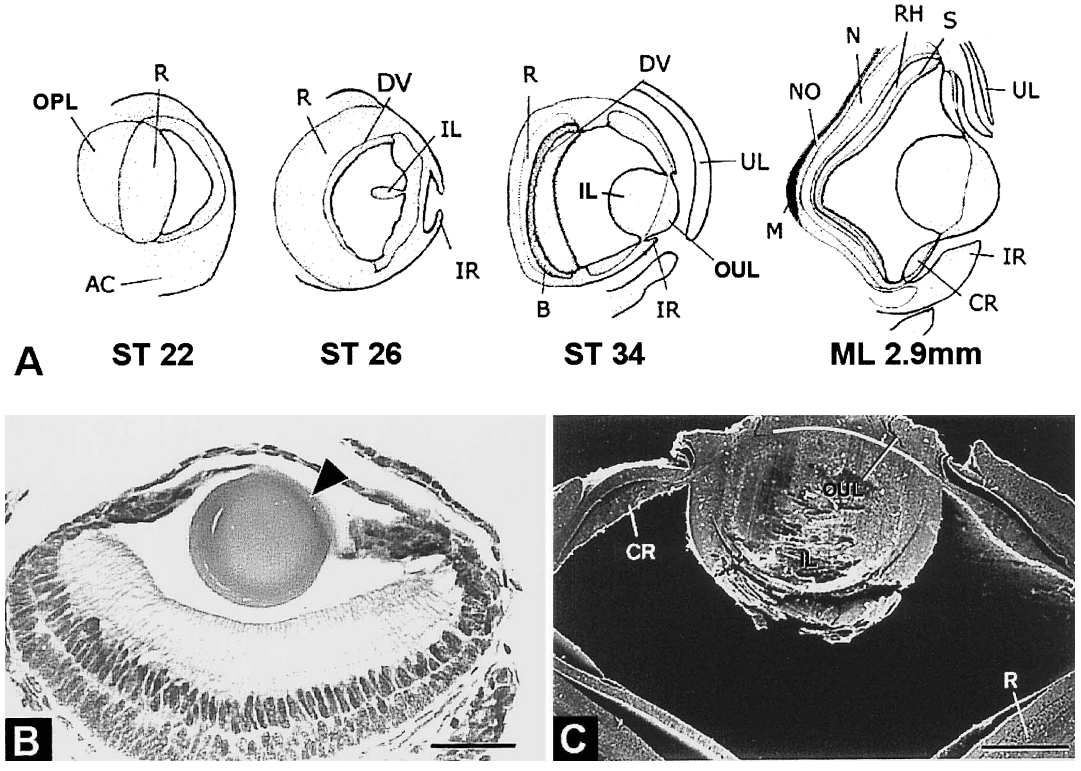


Fig. 12. Development of eye complex of *T. pacificus*. (A) The semi-schematic figures (embryo-paralarval stages 3, ML 2.9mm). Scale differs in each drawing. (B) Eye and segmented lens (paralarval stage 1, St 34; transverse section, HE). The arrowhead indicates the outer lens. (C) The eye vesicle of juvenile (ML 38mm) with the cuboidal inner space and large lens (SEM). The lens is artificially broken during a process of section. A white line demarcates between the outer and inner lenses. AC, anterior chamber organ; B, black pigment layer; CR, lentigen cells; DV, distal segment of visual cell; IL, inner lens; IR, iris; OPL, optic lobe; M, oculomotor muscles; N, nucleated cell body layer; NO, nerve plexus layer; OUL, outer lens; R, retina; RH, rhabdome layer; S, surface layer; UL, upper eyelid. Scale bars, 0.2mm (B), 0.5mm (C).

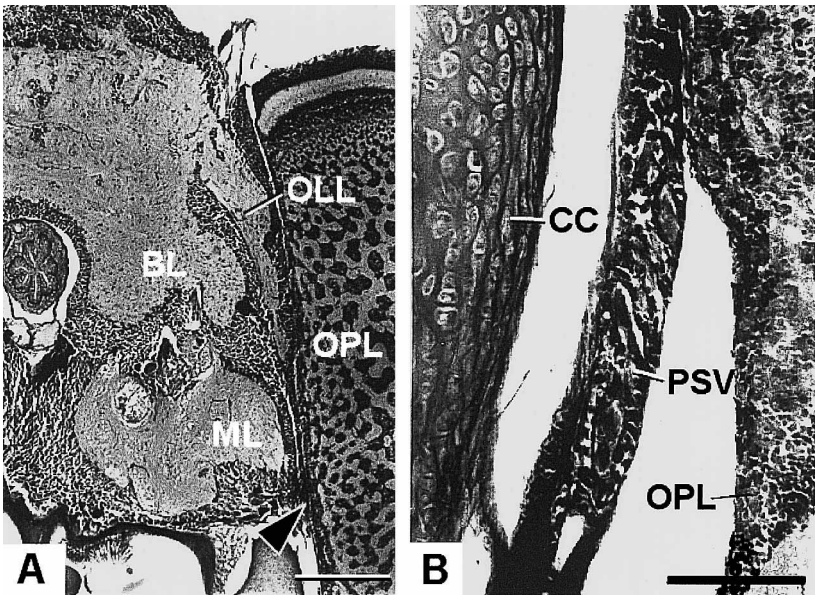


Fig. 13. Histological sections of *T. pacificus*. (A) Position of ventral photosensitive vesicle (arrowhead) and the brain (juvenile, ML 38mm; transverse, Masson). (B) Ventral photosensitive vesicle (the same specimen with figure A). BL, basal lobe; CC, cranial cartilage; ML, magnocellular lobe; OLL, olfactory lobe; OPL, optic lobe; PSV, photosensitive vesicle. Scale bars, 0.3mm (A), 0.2mm (B).

Statoliths first appear on the macula at the anterior parts of statocysts of embryos in St 28. At paralarval stage 1 and 2, statocysts are still ovoid but at the juvenile stage, posterior sac of statocyst become to develop more posteriorly, and straight anticristae and hamuli (hooks) are clearly observed (Fig. 11C). The straight anticristae are longer than hamuli.

Eye parts: They consist mainly of retinal placodes, optic lobes, and anterior chamber organs at the embryonic stage. The retinal placodes are easily recognized as a tight ectodermal layer in St 17 (Watanabe *et al*, 1996). The layer begins to differentiate in St 22, and inner lens are observable in St 26 (Fig. 12A). From St 34 of paralarval stage 1, the outer segments of lens (outer lens) are clearly visible (Fig. 12B). The outer lens and primary eyelids do not appear during a period of embryonic development. Anterior chamber organs ingress from ectodermal cells and begins to be formed around retinal placodes in St 22 (Fig. 12A). The organs are more restricted around the eye at paralarval stage 1 and 2 (Fig. 12B). At the paralarval stage 3, eye vesicles are cuboid in shape compared with the ovoid in the previous stages (Fig. 12C). Retina is fully differentiated with a number of distinct layers.

Ventral photosensitive vesicles: It is difficult to detect the organs during the embryonic and early paralarval stages due to its small numbers of cells. The organs situated at the inner lateral sides of optic lobes are observable at the paralarval stage 3 and at the juvenile stage (Fig. 13A, B). The nerves of the photosensitive vesicles directly run into the neuropil of olfactory lobe. They are distinct with many lobulated vesicles and its most ventral vesicle is larger than dorsal one.

DISCUSSION

Ciliary pattern and type on the epidermis of *T. pacificus* embryos are generally similar to other decabrachian species. Tuft-type cilia arising on the embryonic body and scattered cilia over the outer yolk sac are observed in all decabrachians hitherto reported (Arnold and Williams-Arnold, 1980 in *Loligo pealei*; Boletzky, 1982 in *Loligo vulgaris*, *Sepia officinalis*, *Sepiola robusta*; Sundermann, 1991 in *S. officinalis*; Scharenberg, 1997 in *Alloteuthis media*). However, patches of tuft-type cilia of *T. pacificus* are apparently fewer than other decabrachians (Fig. 1). Typical uniform-type cilia (Arnold and Williams-Arnold, 1980), which occur on both dorsal and ventral surface of mantle in loliginids and a sepiid (e.g. Boletzky, 1982 in *L. vulgaris* and Paulij and Denucé, 1990 in *S. officinalis*), completely lack in *T. pacificus* as well as in a sepiolid species (Boletzky, 1982 in *Sepiola robusta*). In loliginids, the uniform-type cilia are also situated around Hoyle's organ (e.g. Arnold and Williams-Arnold, 1980 in *Loligo pealei*). Similar ciliary distribution in the restricted area around Hoyle's organ is observed in *T. pacificus*. Since the support-type cilia around Hoyle's organ in *T. pacificus* do not exhibit the uniform pattern, it is inconclusive at present if these cilia of *T. pacificus* are corresponding to the uniform-type cilia of other decabrachians. The uniform-type cilia have been proved to work as assistance of the embryos to penetrate the thick outer multilayered jelly of egg case (Boletzky, 1982). Therefore, absence of such kind of cilia in *T. pacificus* may be explained in relation to the substance of its egg case which have loosened gelatinous material of oviducal and nidamental glands origin (Hamabe, 1962; Bower and Sakurai, 1996).

Epidermal ciliary lines of decabrachians are usually recognized as continuous lines on arms and head (*e.g. L. pealei*, Arnold and Williams-Arnold, 1980). However, the epidermal cilia in *Sepiola affinis* are arranged as broad bands or multiple rows except for these in anterior area of dorsal line (along

arm I) and dorsolateral line (along arm II), and overall area of ventral line (along arm IV) (Lenz, *et al.*, 1995). In addition, a broad ciliary band is observed on the ventral side of funnel in *Sepiola affinis* (Lenz *et al.*, 1995). Similar ciliary bands are reported on the epidermis of *Octopus vulgaris* (Lenz, *et al.*, 1995; Lenz, 1997), whereas the cilia on the ventral funnel of the octopus exist as a single continuous line. In *T. pacificus*, all the epidermal ciliary lines exist as broad bands on arm I, II, head, and funnel. On the ventral and lateral sides of proboscis, cilia do not form bands, but scattered. This would relate with small size and weak swimming performance of paralarvae of this species.

Early morphogenesis of digestive organs, namely mid- and hind-gut complex, in *T. pacificus* is primary detected as three swellings at St 25 (Watanabe *et al.*, 1996). In the present study, we showed that these primordia appear as two medioventral mesendodermal clusters on the yolk syncytium at St 19 and three swellings are observed at St 20. Such for-

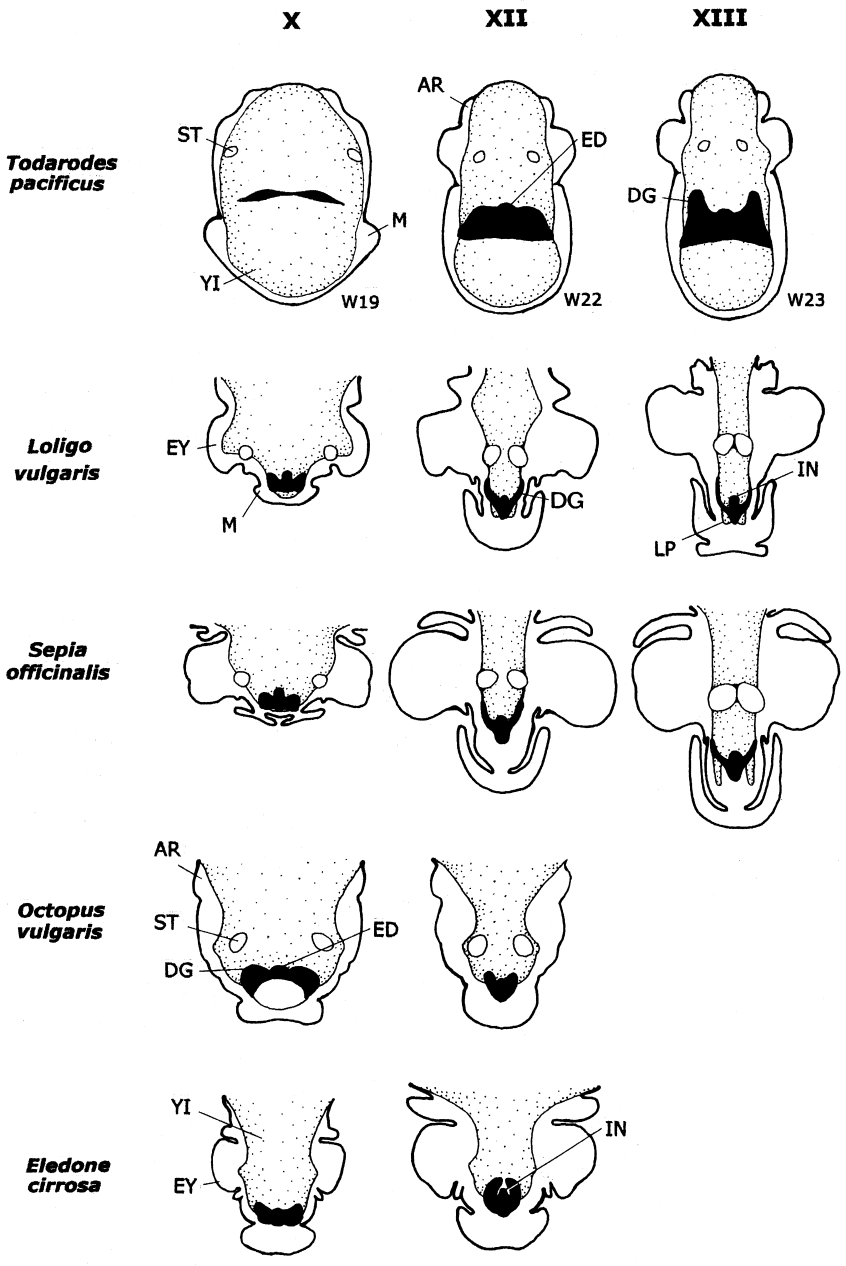


Fig. 14. Comparison of the early development of gut complex in various cephalopod embryos. Solid area shows anlages of gut complex. Roman numerals X, XII, XIII are the embryonic stages of Naef (1928); shell gland almost closes (stage X), funnel folds fuses anteriory (stage XII), and mantle covers the posterior portion of funnel (stage XIII). W19, W22, and W23 indicate the embryonic stages of Watanabe *et al.* (1996) for *T. pacificus*. Except for *T. pacificus*, the outer yolk sac is omitted in the figure. The statocysts of *Eledone cirrosa* are not shown. The original data from *Loligo vulgaris* and *Sepia officinalis* (Meister and Fioroni, 1976), *Octopus vulgaris* (Boletzky, 1967), *Eledone cirrosa* (Fuchs, 1973). AR, arm; DG, digestive gland; ED, endodermal anlage of hindgut; EY, eye; IN, ink sac; LP, posterior lobe of inner yolk; M, mantle; ST, statocyst; YI, inner yolk.

mation process of digestive organs in *T. pacificus* is considerably similar to other coleoids (Boletzky, 1967, 1978; Fuchs, 1973; Opresko, 1974; Meister and Fioroni, 1976). Figure 14 summarized comparison for timing of the differentiation in digestive organs in *T. pacificus* with other coleoid species based on the common developmental stages of Naef (1928). Histological study of *T. pacificus* presently revealed that three mesendodermal swellings occur at St XII, whereas bilateral symmetrical projection of digestive glands are visible at St X in other coleoids (Fig. 14). The differences in timing of its formation certainly indicate a heterochrony. Such retardation in *T. pacificus* reflects the characteristic early feeding mode with weak feeding apparatus such as arm crown and locomotory behavior of the paralarvae, compared to active predators in other neritic species (Boletzky, 1974).

Strong fibers in the funnel retractor muscles of *T. pacificus* are first described in the present study. These fibers would associate to the special behavior of head withdrawal in paralarval stage 1 and 2; when the fibers disappear, the head withdrawal behavior is not observed at the end of paralarval stage 2 (Fig. 15). The head withdrawal behavior is also reported in other ommastrephids *Illex*. A hypothesis for function of such a behavior is that suspensions trapped by the mantle epithelial mucus are transported to the mouth by the motion of head withdrawal (O'Dor, *et al.*, 1985 in *Illex illecebrosus*; Vidal and Haimovici, 1998 in *Illex argentinus*). Since the head withdrawal behavior is also provoked by mechanical (Hamabe 1962) or chemical stimulations (such as formalin, see Okiyama 1965), there is a possibility to appreciate that the head withdrawal may also be a defensive reflex. Therefore disappear of the head withdrawal behavior would not simply mean the end of suspension feeding.

It is difficult to recognize heterochronies in postembryonic phase in *T. pacificus*, because little is known about com-

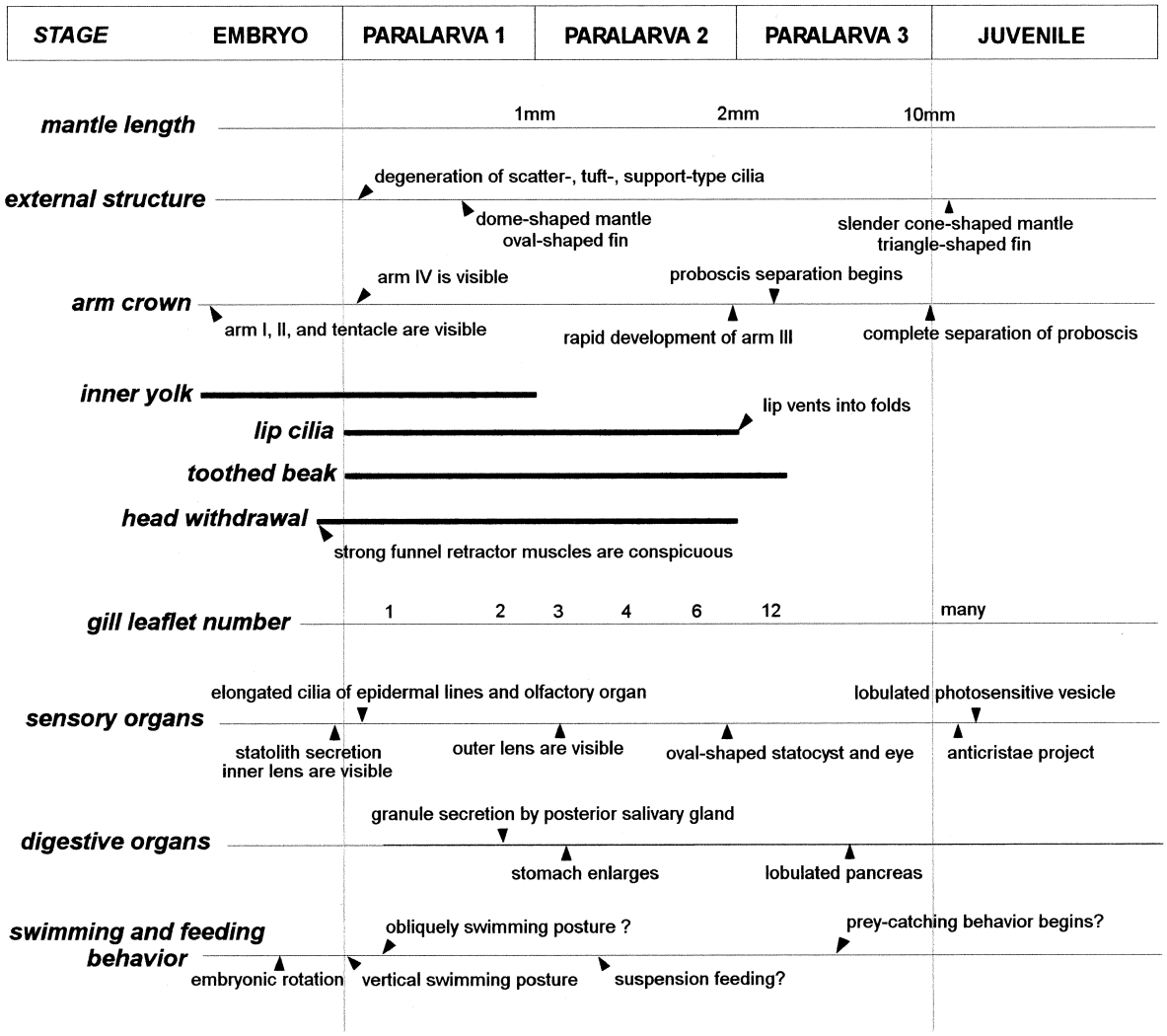


Fig. 15. Early ontogenetic changes of *T. pacificus* from the embryonic stage to juvenile stage. Mantle length is measured from fixed specimens. Data from Hamabe (1962) and Watanabe et al. (1996) are supplementary added for posterior salivary gland, arm development, and gross external form.

parative morphological criteria among different species in coleoids. In general, most organs complete the differentiation during an early period of ontogeny and shift to the allometric growth (Okutani, 1987). In the present study, four stages are tentatively established for the postembryonic development of *T. pacificus*, namely, paralarval 1, 2, 3, and juvenile stage (Fig. 15). Major information on development of the external form, arm crown with suckers, inner yolk, gills is reported by Hamabe (1962) and Watanabe *et al* (1996). We here summarize to consider the early paralarval life with present additional data on the development of selected organs.

Amount of yolk storage is a representative criterion for the paralarval stage 1 of *T. pacificus*. Swimming organs as plankton, such as mantle and funnel are relatively large, but arm crown and sensory organs, such as eye and statocyst are small and immature (Watanabe *et al.*, 1996). As shown in the present study, the olfactory and epidermal cilia grow largely on arms and head, indicating that the paralarvae would be responsible for chemo- and mechanical stimulation. During the paralarval stage 1, arm I, II, and proboscis are not completely formed with the nascent suckers, and arm IV is still bud situation, thus apparatus for prey-catching is quite immature (Watanabe *et al.*, 1996). This indicates that chemosensory information regards as more important than tactile information for paralarvae of this stage. Lip cilia and toothed beak are observed all through this stage. It is considered that the exogenous feeding begins at the late period or end of this stage, since digestive granules are observed in the posterior salivary glands (Watanabe *et al.*, 1996). Many organs of the paralarvae in this stage exhibit a transitory situation from the embryo to "true" paralarva, therefore the paralarvae of this stage may also be called as "planktonic embryo".

Complete absorption of the inner yolk into digestive organs is one of the important criteria to determine the shift of stages from paralarval stage 1 to 2 (Fig. 15). The yolk absorption in paralarval life would certainly relate to the change from endogenous feeding mode to exogenous one (Watanabe *et al.*, 1996). O'Dor *et al.* (1985) hypothesized that rhynchoteuthion paralarvae of *Illex illecebrosus* may perform suspension feeding and the lip cilia are associated such feeding behavior. The lip cilia are present in the paralarva of *T. pacificus* and suspension feeding may be performed in this stage and the ability of head withdrawal into the mantle cavity is observed during the paralarval stage 1 and 2. Small sized and oval shaped eye, and small statocyst without the projection anticristae would support the possibility that paralarvae of this stage are not active predator.

Loss of lip cilia and the development of many folds in the area where the lip cilia previously exist, are one of the major criteria to discriminate the paralarval stage 3. Loss of lip cilia may be related with a change of feeding method. Loss of teeth on the lower beak is not adequate as a main criterion for the paralarval stage 3. Because toothed beak is also observed in planktonic paralarvae of *Octopus vulgaris* and *L. vulgaris* without a drastic change of feeding method even after the toothed beak was lost (Boletzky, 1971). The teeth are considered to work support for bite of larger sized prey (Boletzky, 1971), therefore suspension feeding may not be performed at early period of the paralarval stage 3 of *T. pacificus*. During the period of paralarval stage 3, the separation of proboscis begins at the base, and arm III start to grow rapidly (Watanabe *et al.*, 1996; Fig. 15). Four pairs of arms and a pair of tentacles are thus completed, indicating that prey-capture with arm crown would be regularly performed as feeding behavior.

Complete separation of the proboscis to tentacles had been used as a criterion for the onset of juvenile (Okutani, 1987). Related to the morphological modification of proboscis, the shape of fins changes from oval to triangle. The mantle becomes slender cone-shape, which may indicate the highly swimming activity in the juvenile stage. The eye vesicles are cuboid and considerably large. Thus, most of the characters associated with fast locomotion and accurate feeding represent characteristics as typical nektonic and active predator (Hamabe, 1962).

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