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COMPLETE DEVELOPMENT AND COMPARATIVE MORPHOLOGY OF LARVAL *THENUS ORIENTALIS* AND *THENUS* SP. (DECAPODA: SCYLLARIDAE) REARED IN THE LABORATORY

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ABSTRACT

Newly hatched phyllosomas of 2 species of *Thenus, T. orientalis* and *Thenus* sp., were successfully reared to the juvenile stage under laboratory conditions. Separate cultures of phyllosomas of *T. orientalis* were fed on 4 food regimes consisting of fresh flesh of *Donax brazieri,* frozen flesh of *D. brazieri,* frozen gonad of *Perna canaliculus,* and nauplii of *Artemia.* Phyllosomas of *Thenus* sp. were fed only on fresh flesh of *D. brazieri.* For rearing both species, water temperature was maintained at 27.0 ± 0.5°C. All phyllosomas of the 2 species of *Thenus* fed on fresh flesh of *D. brazieri* developed through 4 phyllosomal instars, equivalent in development to the 4 larval stages of *T. orientalis* previously described from planktonic material. The morphology of these 2 species of *Thenus* at the phyllosomal and nisto stages were compared. The mean number of paired exopodal setae on pereiopods and the total body length of the phyllosomas differed between the two species which were fed fresh flesh of *D. brazieri.* Phyllosomas of *T. orientalis* fed on frozen food (*D. brazieri* or *P. canaliculus*) showed poor survival, prolonged duration of instars, and poor molt increments. Furthermore, approximately 50% of these phyllosomas developed an extra instar (fifth instar) before metamorphosing to the nisto stage. One diagnostic character, the ornamentation of the anterolateral margin of the antennule, was consistent throughout all cultures of both species and identified the larvae of each species. In all instars of *T. orientalis,* there was a short terminal spine on the anterolateral margin of the antennule, whereas in *Thenus* sp. a short seta was present in this position. However, no morphological differences were found to distinguish between the nistos of the two species.

Species of the genus *Thenus* have a wide tropical and subtropical distribution in the Indo-West Pacific region, inhabiting relatively soft, muddy or sandy substrates (George and Griffin, 1972; Barnett *et al.,* 1984; Ito, 1988; Jones, 1988; Kailora *et al.,* 1993). Until recently, all larvae of *Thenus* captured in plankton samples were presumed to belong to the single known species, *Thenus orientalis* (Lund). Prasad and Tampi (1957) described four phyllosomal stages of *T. orientalis,* and gave additional information on laboratory-hatched first stage larvae, thought to be a "prephyllosoma." Johnson (1971) described two phyllosomal stages of *T. orientalis* from the South China Sea, recorded as stage II and "later stage." Prasad *et al.* (1975) reported nine stage of *T. orientalis* based on samples taken throughout the Indian Ocean (see Barnett *et al.,* 1984). Kneipp (1974, cited in Barnett *et al.,* 1984) described five phyllosomal stages, the first two laboratory-reared and stages III, IV, and V from plankton samples. Barnett *et al.* (1984) gave detailed morphological descriptions of four phyllosomal stages of *T. orientalis* taken from the midshelf region of the Great Barrier Reef, and of a nisto stage metamorphosed from a plankton-captured final stage phyllosoma of *T. orientalis.*

Recently, Ito (1988) distinguished two different forms of adult "*T. orientalis*" in Australian waters, one corresponding to *T. orientalis,* which he referred to as *T. orientalis* Form B, and the other which he suggested was a new species and which he referred to as *T. orientalis* Form A. Subsequently, Jones (1988, 1990) working with adult *Thenus,* also recognized two distinct species, *T. orientalis* and *Thenus* sp.A. The new species of *Thenus,* referred to here as *Thenus* sp., is currently being formally described by P. Davie (Queensland Museum, personal communication). *Thenus orientalis* occurs mainly in a depth of 30–60 m of the coastal shelf and offshore areas, over sand and medium-coarse sand between reefs. On the other hand, *Thenus* sp. lives in more turbid inshore coastal water of 10–30-m depth in eastern Queensland (Jones, 1988; Kailora *et al.,* 1993).

Several species of scyllarid lobsters have been reared successfully from hatching to the nisto stage. Robertson (1968) first reported

successful larval development of *Scyllarus americanus* (Smith) through the phyllosomal stage, taking 32–40 days at 25 ± 0.5°C. Takahashi and Saisho (1978) reported complete rearing of phyllosomas of *Ibacus ciliatus* (von Siebold) with seven or eight phyllosomal instars taking 65–72 days at 16–24°C, and of *Ibacus novemdentatus* Gibbes with seven phyllosomal instars taking 65–72 days to the nisto stage at 16–24°C. Ito and Lucas (1990) successfully reared *Scyllarus demani* Holthuis through eight phyllosomal instars and the nisto stage. Phyllosomas of *Ibacus peronii* Leach were reared through six phyllosomal instars at temperatures of 20.7 and 23.3°C, fed on a diet of fresh *Mytilus edulis* Linnaeus (Marinovic *et al.*, 1994). Phyllosomas of *Scyllarus cultrifer* Holthuis were successfully reared to the nisto stage at a temperature of 24°C, being fed chopped gonads of *M. edulis* (in Matsuda and Mikami, unpublished).

In *Thenus,* Ito (1988) reared phyllosomas of *T. orientalis* (=*T. orientalis* Form B) from the egg to the fourth (gilled) instar and phyllosomas of *Thenus* sp. (=*T. orientalis* Form A) up to the second instar at 26–28°C, fed on a diet of nauplii of *Artemia* and fresh flesh of *Gafrarium* sp. Ito (1988) recorded four morphological "stages" in *T. orientalis* as well as "instar" developments and observed several morphological differences in the laboratory-reared early stage (up to the second stage) phyllosomas between these two species. However, no study has successfully reared all larval stages through to the juvenile stage for either of these two species of *Thenus,* and thus complete and direct comparisons between these two species have not previously been possible. The primary aim of this study was to rear larvae of both species of *Thenus* from egg to juvenile, and to determine their morphological distinctions through all larval phases. The secondary aim was to determine whether specific distinctions occur within the species through different feeding treatments.

Materials and Methods

Ovigerous females of *T. orientalis* were obtained from Hervey Bay, south east Queensland, and of *Thenus* sp. from the continental shelf area of the Great Barrier Reef off Cairns, Australia, in 1993. These females were transferred to the QDPI Bribie Island Aquaculture Research Centre and kept in a holding tank with running filtered (20 μm) sea water (33–35‰, 22–27°C). They were fed once daily with flesh from whole frozen New Zealand green mussel, *Perna canaliculus* (Gmelin). When the embryos became amber brown, ovigerous females were removed to individual 200-l hatching tanks until the eggs hatched.

Larvae used in this study originated from females of 6 *T. orientalis* and 2 *Thenus* sp. and hatched during the period from 26 October to 27 December 1993. In each larval rearing, 200 newly hatched phyllosomas were transferred to 10 glass culture bowls (20 phyllosomas per bowl) filled with approximately 1.2 l of sea water at the same salinity as the hatching tanks, with gentle aeration. Rearing sea water was filtered through 1.0- and 0.5-μm cartridge filters. The water was changed twice daily. The culture bowls were placed in water baths and maintained at a constant temperature of 27.0 ± 0.5°C. As the larvae molted through the phyllosomal instars, density in each culture bowl was progressively decreased from the original 20 (first instar) through 10–15 (second instar), 5–8 (third instar), to 1 or 2 larvae (fourth and fifth instars).

Phyllosomas of *T. orientalis* were fed on 4 feeding regimes with a combination of finely chopped frozen gonad of *P. canaliculus,* chopped fresh flesh of *Donax brazieri* Smith, chopped frozen flesh of *D. brazieri,* and cultured nauplii of *Artemia* (from Utah, U.S.A.). Nauplii of *Artemia* were cultured using an *Artemia* diet (Selco, Artemia System SA, Belgium). Appropriate sizes of nauplii of *Artemia* required by successive instars of phyllosomas were: 1 day old for the first phyllosomal instar, 3 days for the second instar, 6 days for the third instar, and 8 days for the fourth instar (Fisheries Research Institute of Mie, unpublished data). Densities of cultured nauplii of *Artemia* in the rearing bowl were maintained at 4 individuals per ml throughout all phyllosomal instars. Phyllosomas of *Thenus* sp. were fed on finely chopped fresh flesh of *D. brazieri.*

Nistos of both species were transferred to a 400-l black polyethylene tank 50 cm deep with a sandy bottom and running sea water (approximately 1.0 l per min) at the same salinity as that in which the ovigerous females had been held. Water temperature was maintained at 25.5–27.0°C. The nistos were not fed during this study.

The phyllosomas, nistos, and exuviae used in descriptions were fixed in sea water 5% Formalin, and preserved in 70% ethyl alcohol. Twenty phyllosomas of each instar, randomly selected from the whole series of samples, were used for examination and description. Measurements and drawings of whole bodies and appendages were made with the aid of a Nikon profile projector and checked microscopically. Various body dimensions of phyllosomas are given as: total body length (TL) measured from the anterior tip of the cephalic shield between the eyestalks to the posterior end of the abdomen (or telson when differentiated); cephalic shield length (CL) measured from the anterior tip to the posterior margin of the cephalic shield; cephalic shield width (CW) measured at the widest part of the cephalic shield; thorax width (TW) measured at the widest part of the thorax; abdomen length (AL) measured from the midline level with the base of the fourth or fifth pereiopod to the posterior end

Table 1. Mean survival (%) to the juvenile stage through phyllosomal and nisto instars of *Thenus orientalis* fed four food regimes and *Thenus* sp. fed fresh flesh of *Donax brazieri*.

Species	Food regime	Phyllosomal instar 1	2	3	4	5	Nisto	Juvenile
Thenus orientalis	FZPG + CAN	100	90	65	20	10	0	0
	FZDF + CAN	100	90	50	10	5	0	0
	FRDF + CAN	100	90	85	77.5	—	75	75
	FRDF	100	100	87.5	82.5	—	80	80
Thenus sp.	FRDF	100	82.5	25	5	—	5	5

CAN = cultured nauplii of *Artemia* (1-day, 3-day, 6-day, and 8-day for first, second, third, and fourth/fifth instar, respectively); FZPG = chopped frozen gonad of *Perna canaliculus*; FRDF = chopped fresh flesh of *D. brazieri*; FZDF = chopped frozen flesh of *D. brazieri*; — = not available.

of the abdomen or telson. The number of pairs of exopodal setae on each pereiopod in each phyllosomal instar was counted with the aid of a binocular microscope. Drawings of the nisto stage were made with the aid of a binocular microscope equipped with a drawing tube. Measurements of nistos were made as total body length (TL) measured from the anterior margin of the antenna to the posterior margin of the telson. Mean values of data derived from the two species were compared using a two-sample *t*-test. Regression equations (least squares method) were calculated between the TL and instar.

The term instar refers to the period of time between two ecdyses. For example, after the first molt a larva would be a second instar larva. The number of instars can only be determined through laboratory observation of larval development. The term "stage" has traditionally been used to describe a distinction based on examination of larvae morphology. One stage may thus involve more than one instar. In the present paper, four phyllosomal stages are recognized (Barnett *et al.*, 1984).

RESULTS

Phyllosomal Instar Growth of *T. orientalis* and *Thenus* sp.

Average survival of phyllosomal and nisto instars of *T. orientalis* fed four food regimes and *Thenus* sp. fed fresh flesh of *D. brazieri* is shown in Table 1. The best survival rates were 100% to the second instar, 87.5% to the third instar, 82.5% to the fourth instar, and 80% to the juvenile stage for *T. orientalis*, and 97.5% to the second, 82.5% to the third, 25% to the fourth, and 5% to the juvenile stage for *Thenus* sp., provided the phyllosomas were fed fresh flesh of *D. brazieri*.

Mean duration of phyllosomal and nisto instars of *T. orientalis* fed four food regimes and *Thenus* sp. fed on fresh flesh of *D. brazieri* in each instar is shown in Table 2. When both species of phyllosomas were fed on fresh flesh of *D. brazieri*, there were no significant differences between the species in mean duration of each instar (*t*-test, $P > 0.05$ in all instars). However, mean duration of instars of phyllosomas of *T. orientalis* fed on frozen gonad of *P. canaliculus* or frozen flesh of *D. brazieri* were more prolonged than those fed on fresh flesh of *D. brazieri* ($P < 0.01$ in each instar).

Details of various body dimensions of phyllosomas and nistos of *T. orientalis* and *Thenus* sp. fed on fresh flesh of *D. brazieri* are presented in Table 3. Mean total body length in each phyllosomal instar of *T. orientalis* was slightly greater than that of *Thenus* sp. in the corresponding instar (*t*-test, $P < 0.05$ in all instars). Regression analysis of total body length (TL) with instar (I) showed the following regression equations:

T. orientalis:

$$TL = 0.293 \times I^3 - 1.070 \times I^2 + 3.967 \times I + 0.700 \quad (P < 0.001)$$

Table 2. Duration (days, mean ± SE) of phyllosomal instars of *Thenus orientalis* reared under four feeding regimes.

Food regime	Phyllosomal instar 1	2	3	4
FZPG + CAN	8.60 ± 0.18	8.46 ± 0.22	12.84 ± 0.41	15.25 ± 0.85
FZDF + CAN	8.41 ± 0.22	8.09 ± 0.14	9.30 ± 0.03	11.53 ± 0.59
FRDF + CAN	6.65 ± 0.10	6.57 ± 0.17	6.42 ± 0.30	7.29 ± 0.24
FRDF	6.65 ± 0.62	6.57 ± 0.50	6.46 ± 0.51	8.39 ± 0.70

CAN = cultured nauplii of *Artemia* (1-day, 3-day, 6-day, and 8-day for first, second, third, and fourth/fifth instar, respectively); FZPG = chopped frozen gonad of *Perna canaliculus*; FRDF = chopped fresh flesh of *Donax brazieri*; FZDF = chopped frozen flesh of *D. brazieri*.

Table 3. Body dimensions (mm) of phyllosomal instars of *Thenus orientalis* and *Thenus* sp. fed on fresh flesh of *Donax brazieri*.

		Instar (number of samples)									
		1 (20)		2 (20)		3 (20)		4 (20)		Nisto (20)	
		TO	TS	TO	TS	TO	TS	TO	TS	TO	TS
TL	mean	3.89	3.67	6.70	6.41	10.89	10.50	18.22	16.44	17.26	17.20
	min.	3.60	3.60	6.10	5.85	10.00	9.90	16.50	13.10	16.20	16.80
	max.	4.08	3.76	7.20	6.90	11.50	11.90	19.80	18.50	18.20	17.90
CL	mean	2.46	2.37	4.48	4.38	7.46	6.77	11.00	10.70	7.20	9.30
	min.	2.08	2.20	4.10	4.95	6.80	6.40	10.10	9.90	6.50	6.80
	max.	2.56	2.84	4.80	4.80	8.20	7.20	12.50	11.50	7.80	7.00
CW	mean	2.95	2.75	5.06	5.20	8.77	6.77	13.16	11.94	9.18	9.10
	min.	2.62	2.50	4.50	4.60	8.00	6.40	11.20	10.50	8.50	8.50
	max.	3.80	2.90	5.60	5.60	9.50	7.20	14.40	13.50	9.80	9.30
TW	mean	1.70	1.54	2.70	2.65	4.52	4.18	6.72	6.30	—	—
	min.	1.54	1.44	5.50	2.40	4.20	3.80	6.00	5.80	—	—
	max.	1.76	1.66	3.00	2.80	4.80	4.40	7.90	6.80	—	—
AL	mean	0.51	0.50	0.75	0.74	1.77	1.64	5.18	4.68	—	—
	min.	0.46	0.42	0.65	0.60	1.50	1.50	4.80	4.20	—	—
	max.	0.56	0.60	0.90	0.90	2.00	1.90	5.90	5.20	—	—

AL = abdomen length; CL = cephalic shield length; CW = cephalic shield width; TL = body length; TO = *T. orientalis*; TS = *Thenus* sp. TW = thorax width; — = not available.

Thenus sp.:

$$TL = 0.088 \times I^3 + 0.175 \times I^2 + 1.832 \times I + 1.780 \ (P < 0.001)$$

Growth rates, expressed as both increments of mean total body length (TL) from one instar (n) to the next (n + 1) and as growth index (increase in mean body length from one instar to the next) are shown in Table 4. Both growth increment and growth index differed slightly between phyllosomas of the two species (*t*-test, $P < 0.05$), with those of *T. orientalis* being greater than those of *Thenus* sp. fed on the same diet of *D. brazieri*.

No major differences in the phyllosomal instar growth have been found between the two species when reared under the same conditions (fed on fresh flesh of *D. brazieri*). However, within species, differences were apparent for phyllosomas of *T. orientalis* when fed different diets. When phyllosomas of *T. orientalis* were fed on either frozen gonad of *P. canaliculus* or frozen flesh of *D. brazieri* with or without the addition of nauplii of *Artemia*, their molt increments in total body length were significantly lower than those fed on fresh flesh of *D. brazieri*, where development was irregular and wide ranges of morphological variation appeared in each phyllosomal instar (Fig. 1).

Furthermore, approximately 50% of fourth instar phyllosomas fed frozen *P. canaliculus* or *D. brazieri* did not develop gill buds and developed to a fifth instar. No fifth instar phyllosomas metamorphosed to the nisto stage. Fourth instar phyllosomas which did not develop gill buds were morphologically equal to stage III phyllosomas except in the segmentation of the antennule. The extra fifth instar phyllosomas were morphologically in agreement with stage IV phyllosomas of *T. orientalis*.

Table 4. Growth (mm, mean ± SE) of phyllosomal instars of *Thenus orientalis* and *Thenus* sp. fed on fresh flesh of *Donax brazieri*.

	Growth increment $TL_{(n+1)} - TL_{(n)}$		Growth index $TL_{(n+1)}/TL_{(n)}$	
Instar	*T. orientalis*	*Thenus* sp.	*T. orientalis*	*Thenus* sp.
1	2.81 ± 0.09	2.74 ± 0.05	1.72 ± 0.03	1.75 ± 0.02
2	4.19 ± 0.15	4.10 ± 0.13	1.63 ± 0.02	1.64 ± 0.02
3	7.33 ± 0.22	7.08 ± 0.24	1.68 ± 0.02	1.68 ± 0.03

TL_n = mean body length in (n)th instar; $TL_{(n+1)}$ = mean body length in (n + 1)th instar.

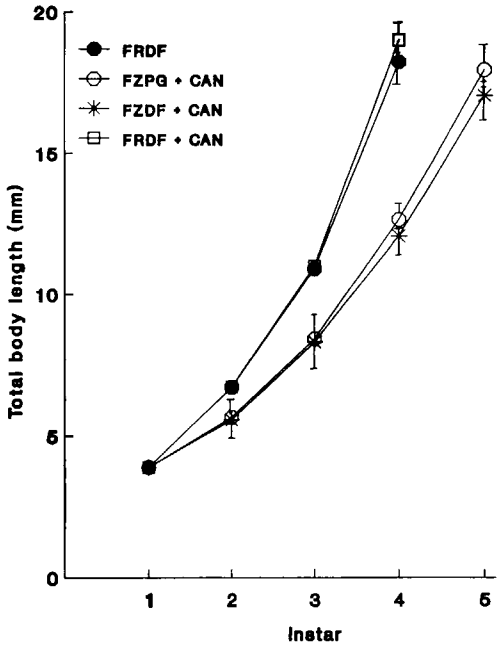

Fig. 1. Relationship between total body length and phyllosomal instar for *Thenus orientalis* fed under different feeding regimes. CAN = cultured nauplii of *Artemia*; FZPG = chopped frozen gonad of *Perna canaliculus*; FZDF = chopped frozen flesh of *Donax brazieri*; FRDF = chopped fresh flesh of *D. brazieri*.

Descriptions of Larval Stages of *T. orientalis* and *Thenus* sp.

A summary of morphological features for phyllosomas of the two species is given in Table 5. Phyllosomas of both species showed substantial morphological changes at each ecdysis, as well as growth in size, and developed through four morphologically clearly defined stages, corresponding to the similar sequence described by Barnett *et al.* (1984), before metamorphosis to the nistos when they were fed on fresh flesh of *D. brazieri*. There were no major morphological differences between the phyllosomas and nisto of the two species, with exceptions as noted in a later section.

Stage I Phyllosoma (Figs. 2, 3).—Eyestalk unsegmented. Antennule unsegmented with 3 long terminal setae, and at inner distal angle 1 very short spine in *T. orientalis* or 1 or 2 seta(e) in *Thenus* sp.; inner ramus rudimentary. Antenna approximately one-third length of antennule, slender, uniramous, terminating in spine with terminal and subterminal setae. Basal segment of first maxilla bearing 3 long coarse terminal spines; coxal segment with 2 elongated coarse terminal spines. Second maxilla single segment, with 2 setules on anterior margin, bearing 3 long plumose setae. Second maxilliped of 4 segments without exopod. Third maxilliped bearing ventral coxal spine and comblike setae on terminal segment. Average number of pairs of exopodal setae on first to fourth pereiopods: 14.9:15.7:15.5:0.8 pairs in *T. orientalis* and 16.8:17.6:16.7:0.7 pairs in *Thenus* sp. (20 specimens fed on fresh flesh of *D. brazieri* examined for each species). Fifth pereiopod elongated bud, parallel to abdomen and about two-thirds length of abdomen. Ventral coxal spines with accessory seta on third maxilliped and first to fourth pereiopods. Subexopodal spines on first to fourth pereiopods. Tiny ventral thoracic spines adjacent to coxa of third maxilliped and first to fourth pereiopods. Uropod rudimentary bud. Posterolateral spine with 3 basal setae on each side of distal end of abdomen.

Stage II Phyllosoma (Figs. 4, 5).—Eyestalk segmented. Antennule segmented; first segment well developed; second segment bearing 4 long setae and 3 or 4 groups of sensory setae, and at inner distal angle, 1 very short spine with 1 or 2 seta(e) in *T. orientalis* or 2 or 3 setae in *Thenus* sp. Antenna bifurcate, one-half length of antennule; lateral process short. Basal segment of first maxilla bearing 3 long coarse terminal spines; coxal segment bearing 2 elongated coarse terminal spines. Second maxilla single paddle-shaped lobe with 2 setules on anterior margin. First maxilliped small bud at base of second maxilla. Second maxilliped of 4 segments without exopod. Average number of pairs of exopodal setae on first to fourth pereiopods: 19.3:19.7:19.4:10.3 in *T. orientalis* and 21.4:22.5:21.2:12.0 in *Thenus* sp. (20 specimens fed on fresh flesh of *D. brazieri* examined). Fifth pereiopod twice length of abdomen, with 2 or 3 segments; distal segment terminating in 1 or 2 short spines. Pleopods absent. Posterolateral spine plus 3 setae on each rounded corner of telson. Uropod bifurcate.

Stage III Phyllosoma (Figs. 6, 7).—Antennule of 4 segments; third segment elongated; fourth segment bearing 4 long setae, 9–12 groups of sensory setae, and, at inner distal angle, 1 very short spine with 2 or 3 setae in

Table 5. Summary of morphological development of phyllosomas of *Thenus orientalis* and *Thenus* sp.

Features	spp. + food	Instar 1	2	3	4	5
Eyestalk	TSD	unseg	seg	seg	seg	—
	TOD	=	=	=	=	—
	TOP	=	=	=	=	seg
Antennule	TSD	biram, unseg	biram, 1-seg	biram, 4-segs	biram, 4 segs	—
	TOD	=	=	=	=	—
	TOP	=	=	=	=	biram, 4-segs
Antenna	TSD	uniram, unseg	biram, unseg	biram, unseg	biram, 2-segs	—
	TOD	=	=	=	=	—
	TOP	=	=	=	=	biram, 2-segs
2nd Maxilla	TSD	3-ts	lost ts, lobe	lobe	developed lobe	—
	TOD	=	=	=	=	—
	TOP	=	=	=	=	developed lobe
Maxilliped 1	TSD	absent	absent	bud	bilobed	—
	TOD	=	=	=	=	—
	TOP	=	=	=	=	bilobed
Maxilliped 2	TSD	5-segs	5-segs	5-segs	+exop bud	—
	TOD	=	=	=	=	—
	TOP	=	=	=	+rud exop bud	+exop bud
Maxilliped 3	TSD	5-segs	5-segs	+rud exop bud	+exop bud	—
	TOD	=	=	=	=	—
	TOP	=	=	=	=	+exop bud
Pereiopod 4	TSD	5-segs, exop	set exop			
	TOD	bud (occasionally	=	=		
	TOP	with setae)	=			
Pereiopod 5	TSD	bud	2-segs	5-segs	5-segs	—
	TOD	=	=	=	=	—
	TOP	=	=	=	=	5-segs
Pleopods	TSD	absent	absent	small bud	uniram bud	—
	TOD	=	=	=	=	—
	TOP	=	=	absent	rud	bud
Uropods	TSD	bud	biram (<abd)	biram (>tel)	seg	—
	TOD	=	=	=	=	—
	TOP	=	=	=	unseg	seg
Telson	TSD	undiff	undiff	diff	diff	—
	TOD	=	=	=	=	—
	TOP	=	=	=	=	diff
Gill buds	TSD	absent	absent	absent	present	—
	TOD	=	=	=	=	—
	TOP	=	=	=	50% present	complete

TOD = *T. orientalis* fed on fresh flesh of *Donax brazieri*; TOP = *T. orientalis* fed on frozen gonad of *Perna canaliculus* and nauplii of *Artemia*; TSD = *Thenus* sp. fed on fresh flesh of *D. brazieri*; abd = abdomen; biram = biramous; diff = differentiated; exop = exopod; rud = rudimentary; seg = segmented; segs = segments; set exop = setose exopod; ts = terminal setae; undiff = undifferentiated; uniram = uniramous; unseg = unsegmented; — = not available; = = same as above.

T. orientalis or 2 or 3 setae in *Thenus* sp. Antenna bifurcate and flattened, approximately one-half length of antennule; inner process terminating in acute spinous process with 3 teeth; outer process enlarged and expanded with outer margin slightly serrated with 3 teeth. Basal segment of first maxilla bearing 4 long coarse terminal spines; coxal segment bearing 2 elongated coarse terminal spines and additional spinule subterminally. Second maxilla enlarged, bifurcation as indicated, expanded posteriorly with 2 setules on anterior margin. First maxilliped slightly elongated rudimentary bud. Second maxilliped of 4 segments without exopod. Average number of pairs of exopodal setae on first to fourth pereiopods: 22.2:22.5:22.0:16.5 in *T. orientalis* and 26.0:26.1:24.9:19.7 pairs in *Thenus* sp. (20 specimens fed on fresh flesh of *D. brazieri* examined). Fifth pereiopod twice

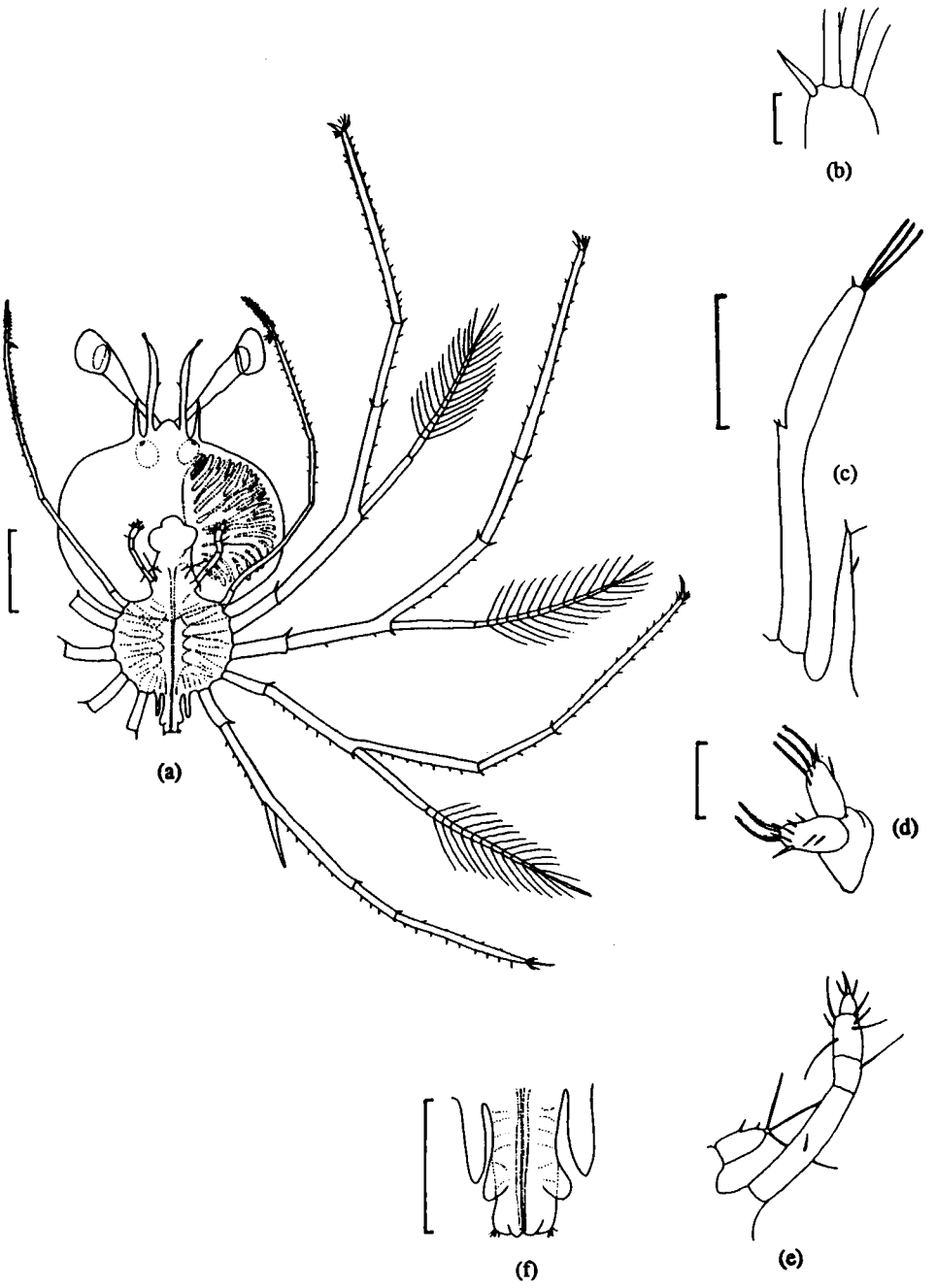

Fig. 2. *Thenus orientalis,* first instar phyllosoma. (a) ventral view; (b) distal end of left antennule; (c) left antennule and antenna; (d) left first maxilla; (e) left second maxilla and second maxilliped; (f) abdomen and fifth pereiopods. Scale bars: a = 1 mm; b = 50 μm; c = 0.5 mm; d = 0.25 mm; e, f = 0.5 mm.

length of abdomen, with 5 segments. Four pairs of pleopods as small bud or sometimes absent. Uropods well developed but unsegmented, reaching posterior margin of telson.

Stage IV Phyllosoma (Figs. 8, 9).—Antennule of 4 segments; third segment elongated and slightly longer than fourth segment; fourth segment bearing 4 long setae, 12–14 groups

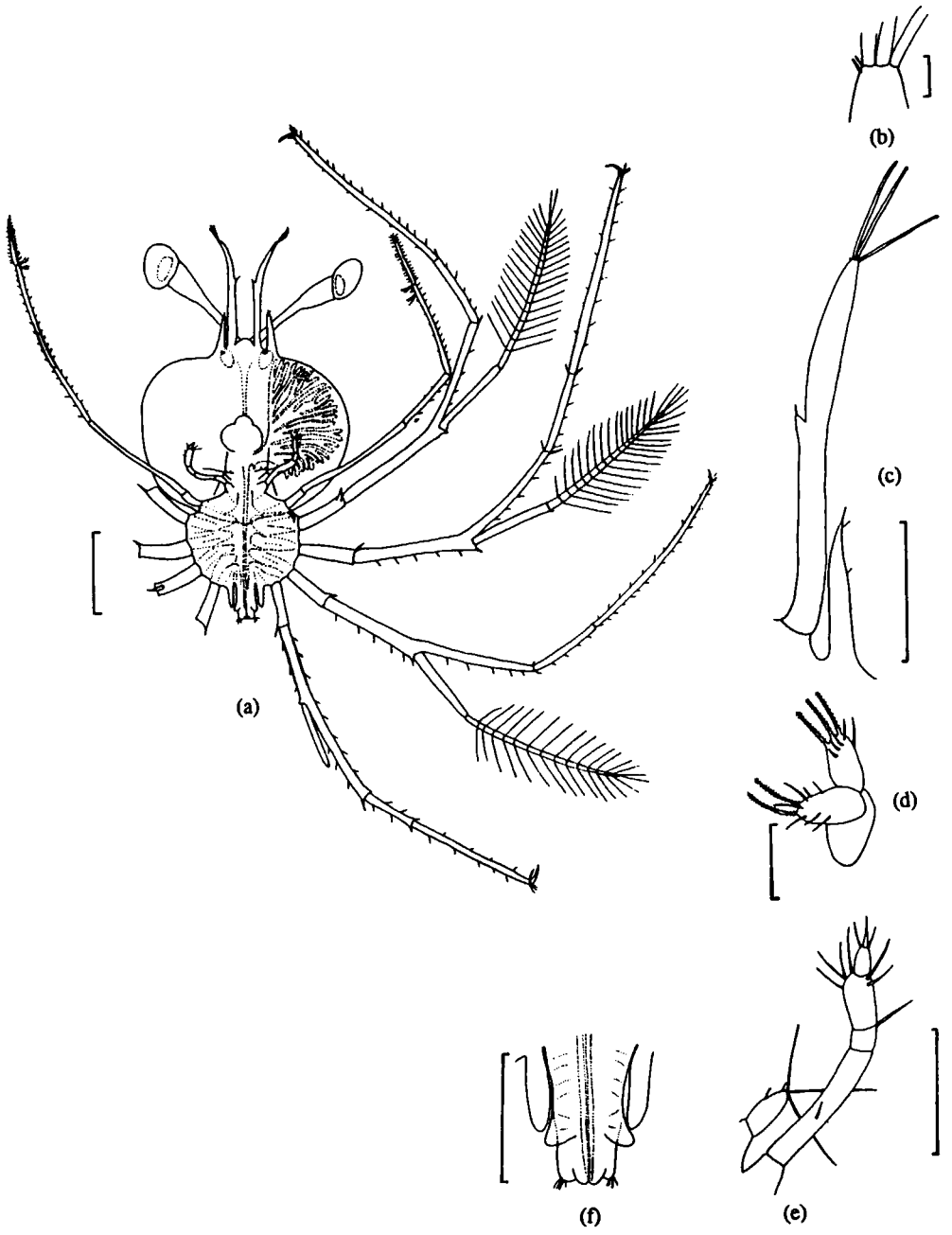

Fig. 3. *Thenus* sp., first instar phyllosoma. (a) ventral view; (b) tip of left antennule; (c) left antennule and antenna; (d) left first maxilla; (e) left second maxilla and second maxilliped; (f) abdomen and fifth pereiopods. Scale bars: a = 1 mm; b = 50 μm; c = 0.5 mm; d = 0.25 mm; e, f = 0.5 mm.

of sensory setae and at inner distal angle, 1 very short spine with 2 or 3 setae in *T. orientalis* or 2 or 3 setae in *Thenus* sp. Antenna bifurcate and flattened, segmented or with indication of segmentation, three-fourths length of antennule; inner process serrated with 4 or 5 teeth on inner margin and 3 or 4 teeth on outer margin; outer process serrated with 3 or 4 teeth on outer margin. Basal segment of first maxilla bearing 4 long coarse termi-

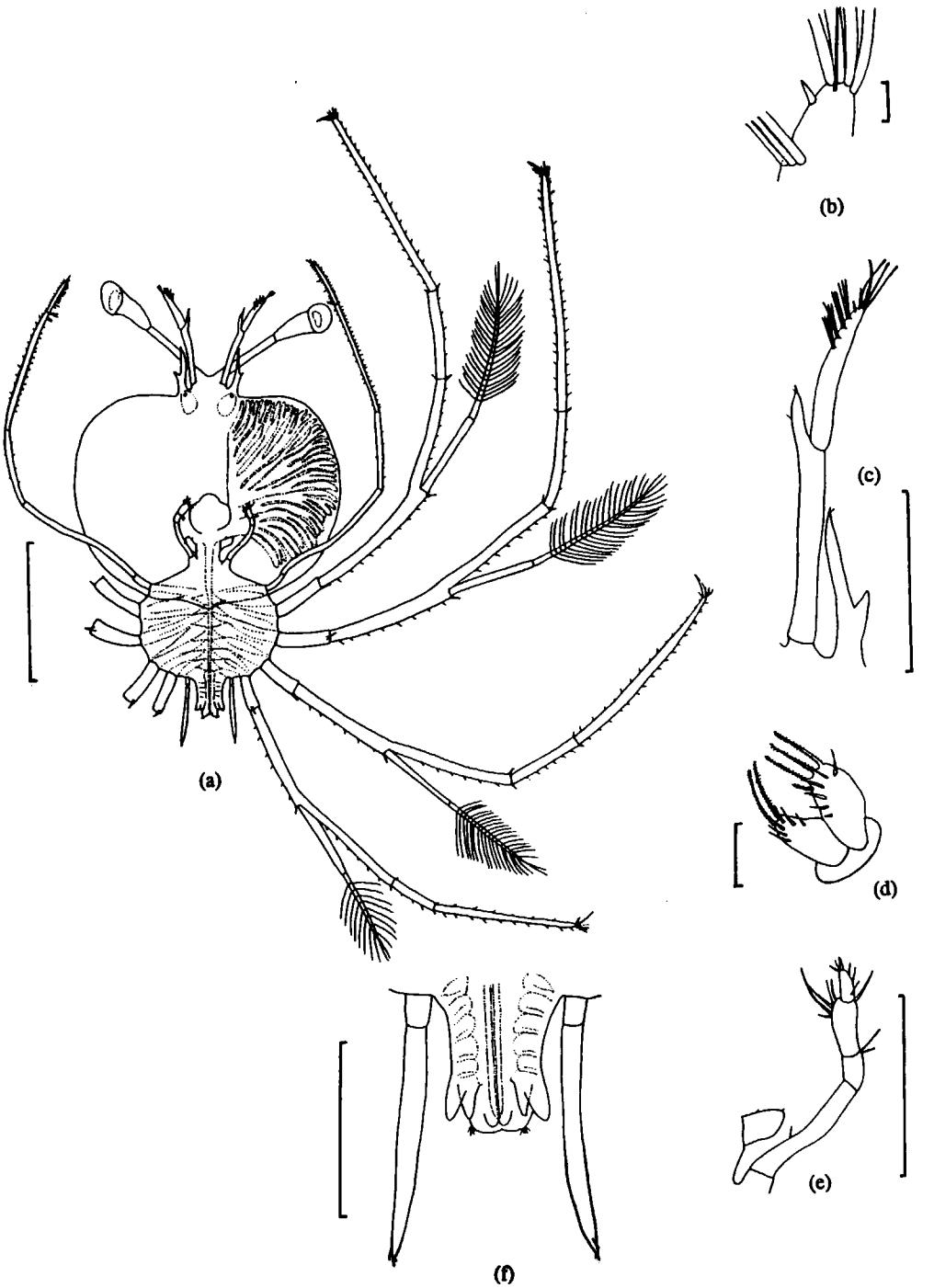

Fig. 4. *Thenus orientalis*, second instar phyllosoma. (a) ventral view; (b) tip of left antennule; (c) left antennule and antenna; (d) left first maxilla; (e) left second maxilla and second maxilliped; (f) abdomen and fifth pereiopods. Scale bars: a = 2.5 mm; b = 50 μm; c, e, f = 1.0 mm; d = 0.1 mm.

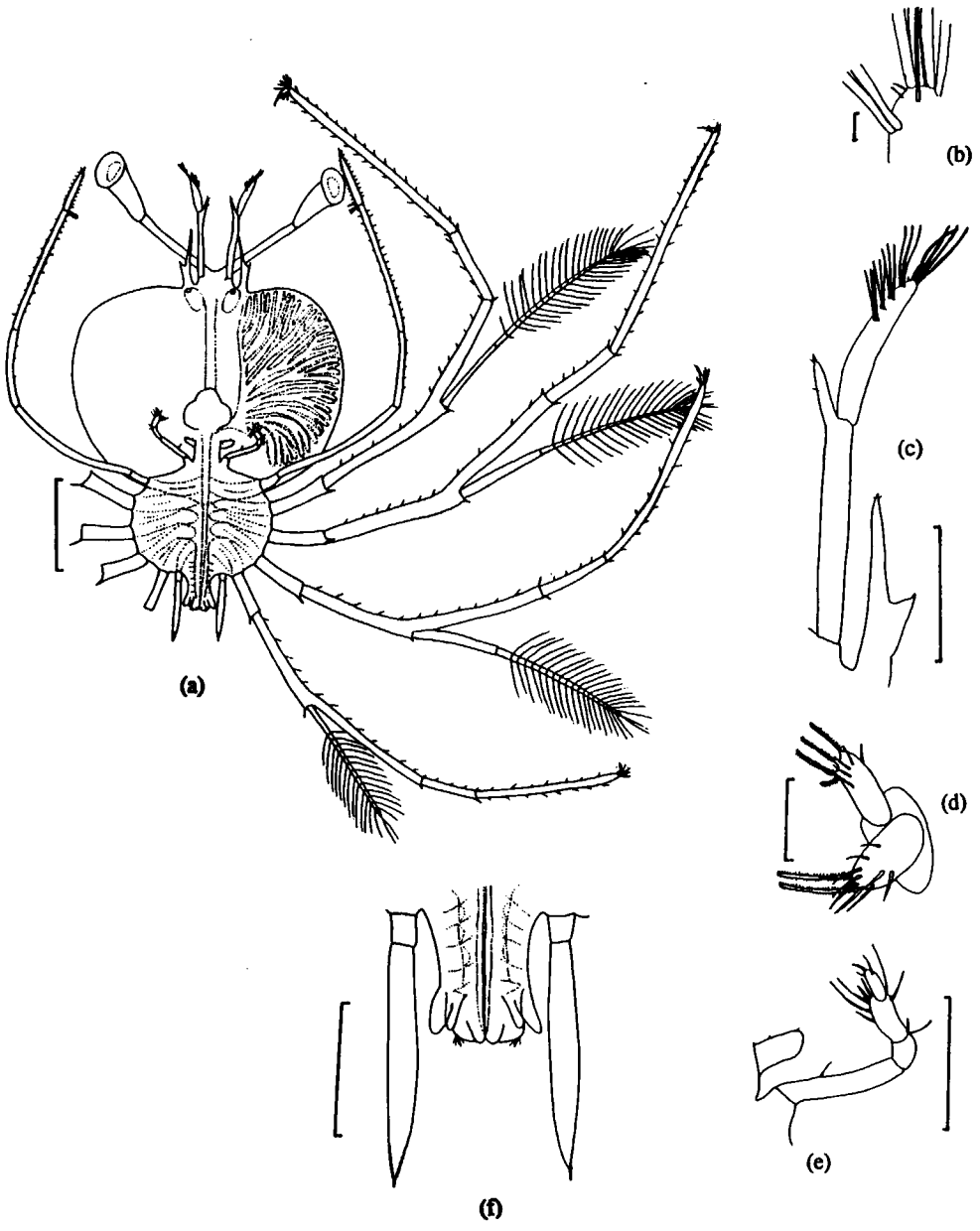

Fig. 5. *Thenus* sp., second instar phyllosoma. (a) ventral view; (b) tip of left antennule; (c) left antennule and antenna; (d) left first maxilla; (e) left second maxilla and second maxilliped; (f) abdomen and fifth pereiopods. Scale bars: a = 2.5 mm; b = 50 μm; c, e, f = 1.0 mm; d = 0.1 mm.

nal spines and 1 short coarse terminal spine; coxal segment bearing 2 elongated coarse terminal spines and 1 short coarse terminal spine. Second maxilla enlarged, flattened, and trilobed. First maxilliped bifurcate, with fingerlike process. Second maxilliped of 4 segments with exopod bud on first segment. Average number of pairs of exopodal setae on first to fourth pereiopods: 25.2:25.5:24.8:20.4 in *T. orientalis* and 28.3:28.8:28.8:23.7 pairs in *Thenus* sp. (20 specimens fed on fresh flesh of *D. brazieri* examined). Fifth pereiopod twice length of abdomen, with 5 segments. Gill buds on dorsal side of basal segment of

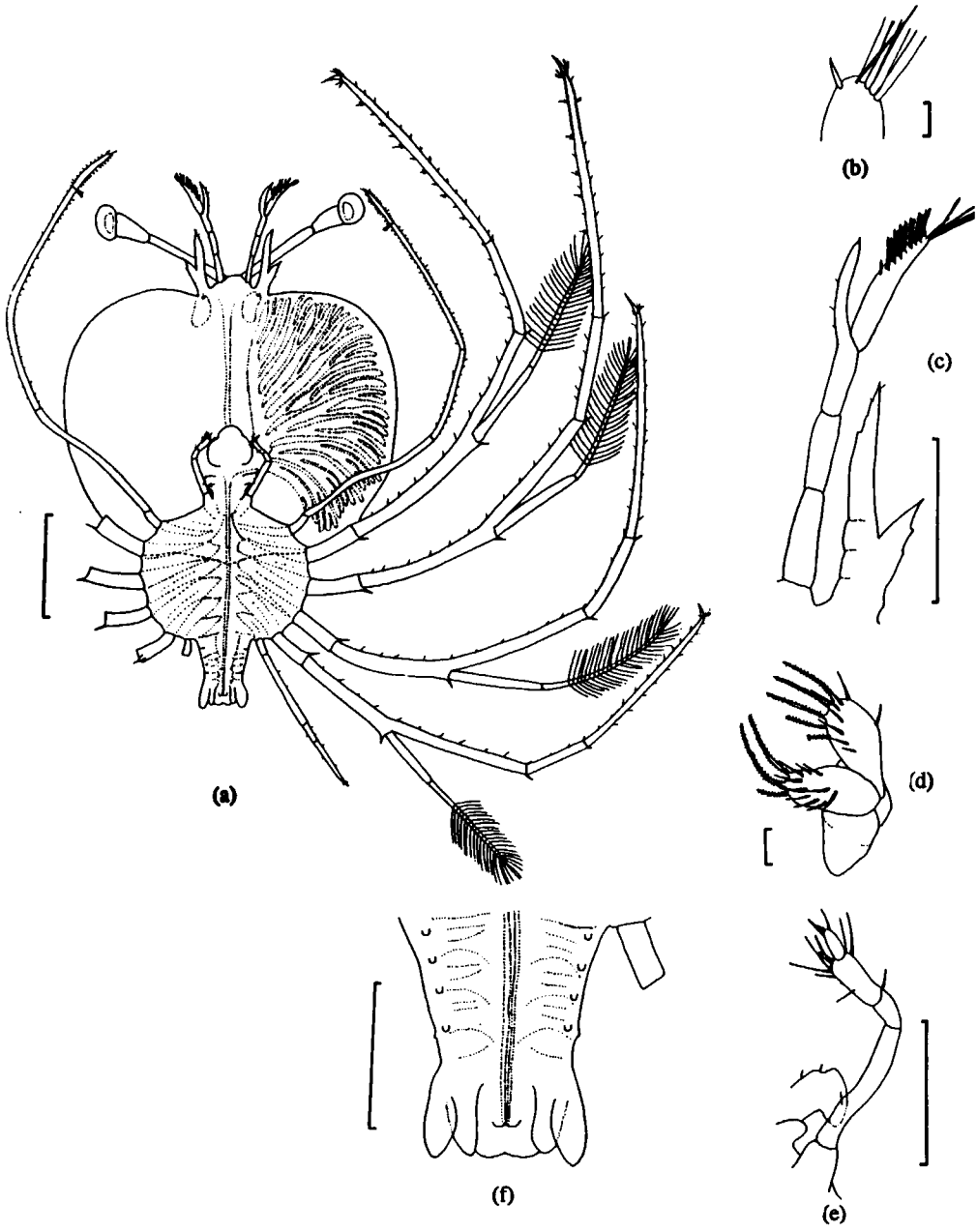

Fig. 6. *Thenus orientalis*, third instar phyllosoma. (a) ventral view; (b) tip of left antennule; (c) left antennule and antenna; (d) left first maxilla; (e) left second maxilla and second maxilliped; (f) abdomen and fifth pereiopods. Scale bars: a = 2.5 mm; b = 50 μm; c, e, f = 1.0 mm; d = 0.1 mm.

third maxilliped and first to fourth pereiopods, and on thorax near margin adjacent to third maxilliped and first to fourth pereiopods. Four pairs of pleopods as small uniramous buds. Uropods segmented, extending beyond posterior margin of telson.

Nisto (Fig. 10).—Short blunt spine on midpoint of anterior margin with second spine posterior to it. Middorsal ridge broken line bounded laterally by small anteriorly directed spines. Short lateral ridge extending obliquely from supraorbital region to below angle of

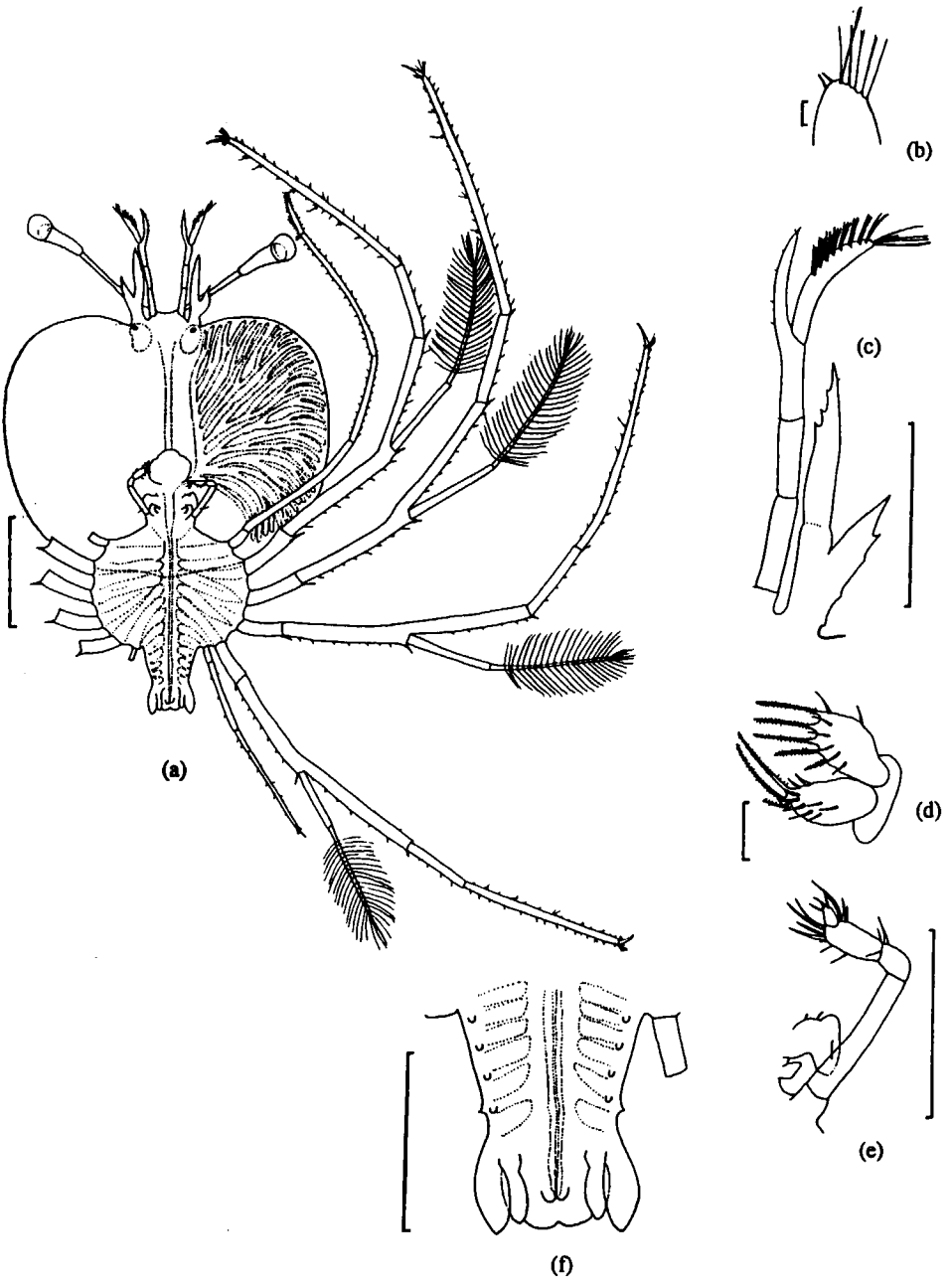

Fig. 7. *Thenus* sp., third instar phyllosoma. (a) ventral view; (b) tip of left antennule; (c) left antennule and antenna; (d) left first maxilla; (e) left second maxilla and second maxilliped; (f) abdomen and fifth pereiopods. Scale bars: a = 2.5 mm; b = 50 μm; c, e, f = 1.0 mm; d = 0.1 mm.

eye orbit. Two lateral lines of short spines extending along brachial region to posterior margin. Carapace surface covered with fine hairs. Lateral margin of carapace serrulate with 1 prominent notch followed by 2 smaller notches posterior to orbit. Eyes at anterolateral angle of carapace, framed by spinose, V-shaped orbit. Antennule of 4 segments; second segment elongated and longer than first segment; third segment bearing sensory se-

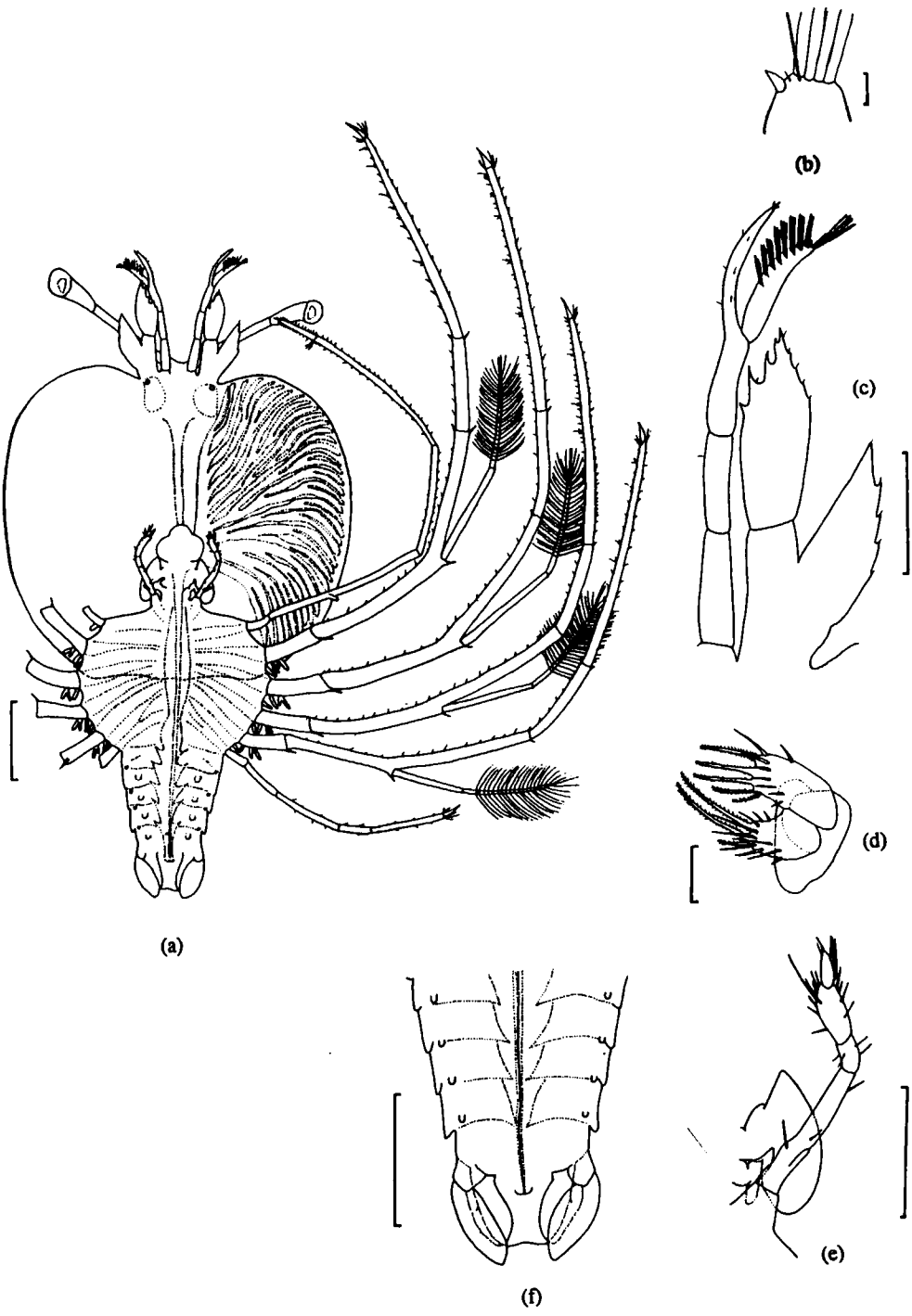

Fig. 8. *Thenus orientalis,* fourth instar phyllosoma. (a) ventral view; (b) tip of left antennule; (c) left antennule and antenna; (d) left first maxilla; (e) left second maxilla and second maxilliped; (f) abdomen and fifth pereiopods. Scale bars: a = 2.5 mm; b = 50 μm; c, e, f = 2.0 mm; d = 0.1 mm.

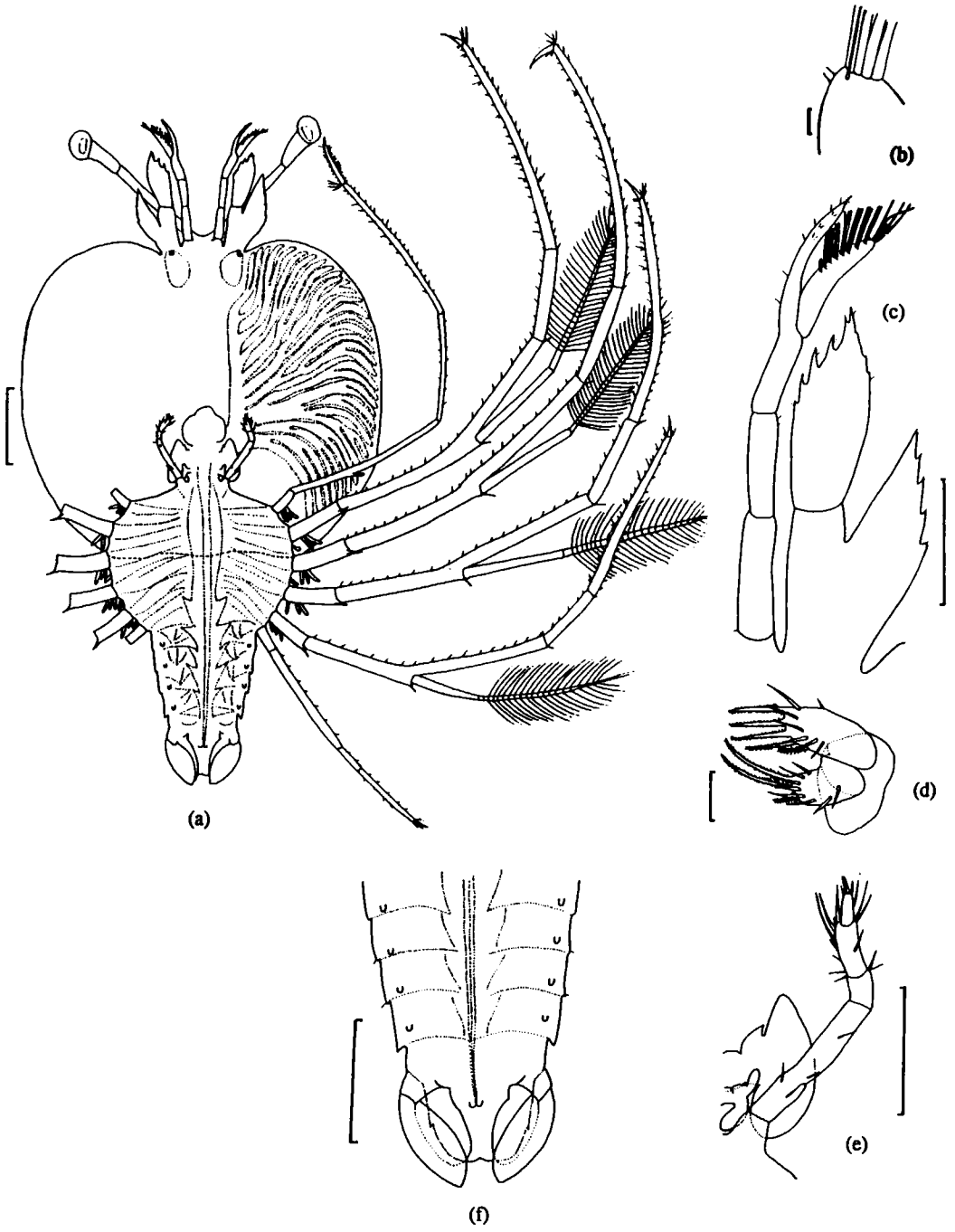

Fig. 9. *Thenus* sp., fourth instar phyllosoma. (a) ventral view; (b) tip of left antennule; (c) left antennule and antenna; (d) left first maxilla; (e) left second maxilla and second maxilliped; (f) abdomen and fifth pereiopods. Scale bars: a = 2.5 mm; b = 50 μm; c, e, f = 2.0 mm; d = 0.1 mm.

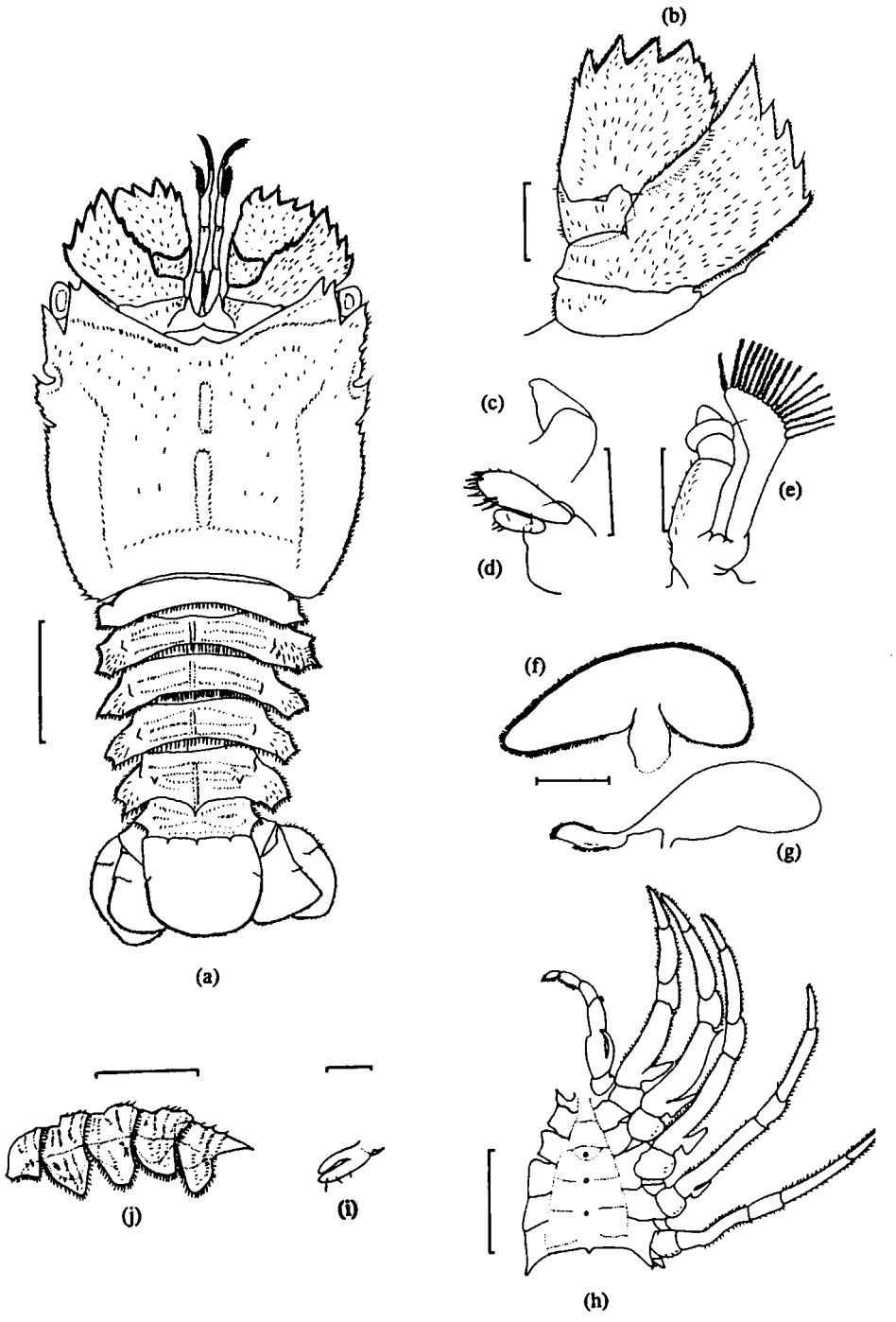

Fig. 10. *Thenus orientalis*, nisto instar. (a) dorsal view; (b) dorsal view of right antenna; (c) left mandible; (d) left first maxilla; (e) left second maxilliped; (f) left second maxilla; (g) left first maxilliped; (h) ventral view of left first third maxilliped, pereiopods 1–5 and thoracic sterna; (i) left first pleopod; (j) lateral view of abdominal pleura of somites 1–6 and middorsal carinae of somites 2–5. Scale bars: a = 2.0 mm; b, c, d, e, f, g = 1.0 mm; h = 2.0 mm; i = 0.1 mm; j = 2.0 mm.

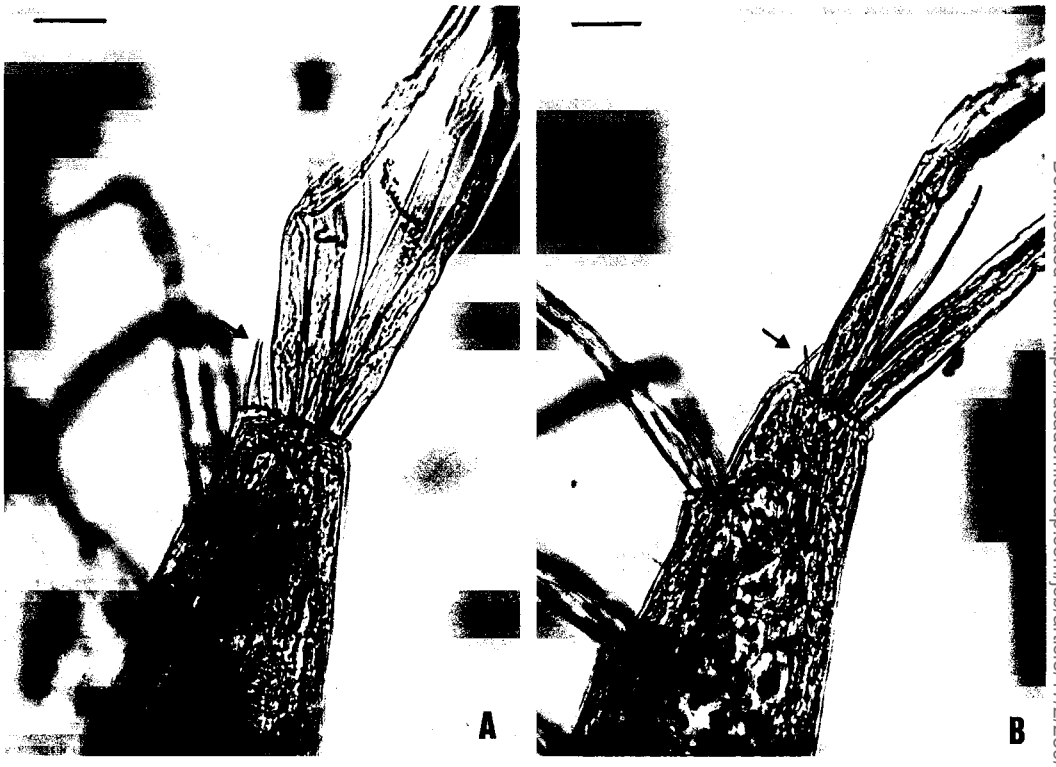

Fig. 11. Differences on the anterolateral margin of the antennule of the second instar phyllosoma of (A) *Thenus orientalis* and of (B) *Thenus* sp. Arrows indicate (A) the terminal spine and (B) the setae. Scale bars: A, B = 50 μm.

tae; fourth segment bearing setae. Antenna of 4 segments; anterior margin of fourth (distal) segment with 9 or 10 teeth on outer margin; outer margin of second segment with 4 or 5 teeth. Mandibles with nonsetose palp. Second maxilla flattened with marginal setae. First maxilliped flattened; distal segment flattened with setae on margin. Second maxilliped of 4 segments with exopod on first segment; exopod elongated and slightly longer than endopod; distal end of exopod flattened, bearing plumose setae on distal margin. Third maxilliped of 5 segments with short exopod on first segment; distal margin of carpus and dactylus setose. All pereiopods bearing setae; basis of first to fourth pereiopods with vestigial exopod. Pleopods biramous with 3 short setae on exopod. Pleura of second to fourth abdominal segments angular and serrulate. Pleura of fifth segment with posteriorly directed angular projection. Telson with marginal setae. Uropod extending beyond posterior margin of telson, with marginal setae.

Morphological Differences between the Phyllosomas and Nistos of the Two Species of *Thenus*

The only consistent morphological difference found between phyllosomas of the two species concerned ornamentation of the distal end of the antennule. In *T. orientalis* there is a short terminal spine with 1–3 short seta(e) on the anterolateral margin of the antennule, whereas in *Thenus* sp. only one seta (first instar) or 2 or 3 short setae (second, third, and fourth instar) are present in this position and a terminal spine is not observed (Fig. 11). After metamorphosis to the nisto instar, these characteristics disappear and morphological separation of the two species is not possible.

As noted earlier, body size was greater in all phyllosomal instars of *T. orientalis* than in *Thenus* sp., even when reared under identical conditions. Similarly, under these identical conditions there were statistical differences between the two species in the num-

Table 6. Comparison of numbers (mean ± SE) and range (in parentheses) of pairs of natatory setae on the exopod of pereiopods 1–4 in each phyllosomal instar of *Thenus orientalis* and *Thenus* sp.

Instar	Species	Food regime	Pereiopod 1	Pereiopod 2	Pereiopod 3	Pereiopod 4
	T. orientalis	FZPG + CAN	14.93 ± 0.11[a] (13–16)	15.67 ± 0.09[a] (14–17)	14.52 ± 0.08[a] (13–16)	0.76 ± 0.17[a] (0–3)
1	*T. orientalis*	FRDF	14.93 ± 0.11[a] (13–16)	15.67 ± 0.09[a] (14–17)	14.52 ± 0.08[a] (13–16)	0.76 ± 0.17[a] (0–3)
	Thenus sp.	FRDF	16.82 ± 0.06[b] (16–18)	17.60 ± 0.07[b] (17–18)	16.65 ± 0.08[b] (16–18)	0.73 ± 0.06[a] (0–1)
	T. orientalis	FZPG + CAN	18.80 ± 0.09[a] (18–19)	19.65 ± 0.17[a] (18–21)	18.52 ± 0.11[a] (18–19)	9.85 ± 0.23[a] (8–12)
2	*T. orientalis*	FRDF	19.25 ± 0.12[b] (18–21)	19.70 ± 0.11[a] (19–18)	19.35 ± 0.13[b] (18–20)	10.25 ± 0.16[b] (9–12)
	Thenus sp.	FRDF	21.40 ± 0.11[c] (21–22)	22.50 ± 0.14[b] (21–23)	21.15 ± 0.17[c] (20–22)	11.95 ± 0.17[c] (11–13)
	T. orientalis	FZPG + CAN	22.10 ± 0.10[a] (22–23)	22.40 ± 0.16[a] (22–23)	21.50 ± 0.71[a] (21–23)	16.30 ± 0.26[a] (15–18)
3	*T. orientalis*	FRDF	22.20 ± 0.20[a] (22–23)	22.50 ± 0.22[a] (21–23)	22.00 ± 0.15[b] (21–23)	16.50 ± 0.31[a] (15–18)
	Thenus sp.	FRDF	26.00 ± 0.15[b] (25–27)	26.10 ± 0.18[b] (25–27)	24.90 ± 0.18[c] (24–26)	19.70 ± 0.21[b] (19–21)
	T. orientalis	FZPG + CAN	23.60 ± 0.34[a] (22–25)	23.70 ± 0.34[a] (22–26)	23.30 ± 0.30[a] (22–24)	19.10 ± 0.48[a] (16–21)
4	*T. orientalis*	FRDF	25.20 ± 0.13[b] (25–26)	25.50 ± 0.17[b] (25–26)	24.80 ± 0.13[b] (24–25)	20.40 ± 0.16[b] (20–21)
	Thenus sp.	FRDF	28.30 ± 0.15[c] (28–29)	28.80 ± 0.25[c] (28–30)	28.80 ± 0.20[c] (28–30)	23.70 ± 0.30[c] (23–26)

CAN = cultured nauplii of *Artemia* (1-day, 3-day, 6-day, and 8-day for first, second, third, and fourth/fifth instar, respectively); FZPG = chopped frozen gonad of *Perna canaliculus*; FRDF = chopped fresh flesh of *Donax brazieri*. Means with the same superscripts in the same column within an instar are not significantly different ($P > 0.05$).

ber of pairs of exopodal setae on the pereiopods (Table 6). Frequency distributions of the number of pairs of exopodal setae on each pereiopod of *Thenus* sp. were significantly higher (*t*-test, $P < 0.05$) than those of *T. orientalis* throughout all phyllosomal instars, except for the fourth pereiopod in the first instar (*t*-test, $P > 0.5$). However, there are statistical variances of these frequency distributions in late instar phyllosomas within the species when comparisons are made on larval groups fed on different diets (fresh flesh of *D. brazieri* versus frozen gonad of *P. canaliculus* (Table 6)).

Discussion

This study provides the first opportunity to describe morphological features of phyllosomas of *T. orientalis* and *Thenus* sp. reared under laboratory conditions.

Larval Development of *T. orientalis* and *Thenus* sp.

Barnett *et al.* (1984) described four phyllosomal stages and one nisto stage of *T. orientalis* based on specimens from plankton samples taken over the shelf areas of the Great Barrier Reef, and made an attempt to clarify discrepancies in the existing literature related to the descriptions of phyllosomas of *Thenus*, including works by Prasad and Tampi (1957), Johnson (1971), Kneipp (1974, cited in Barnett *et al.*, 1984), and Prasad *et al.* (1975). Furthermore, Ito (1988) attempted rearing of phyllosomas of both *T. orientalis* and *Thenus* sp. and successfully developed phyllosomas of *T. orientalis* up to the fourth (gilled) instar and *Thenus* sp. up to the second instar. From similarities in the rate of development to the second instar in the two species, and the degree of development to the fourth instar of *T. orientalis*, Ito (1988) concluded that both species probably had only four developmental instars as well as the four morphological stages, as described in Barnett *et al.* (1984), before metamorphosis to the nisto instar.

The present rearing experiments confirm that for both species, when the diet is adequate, four phyllosomal instars precede the

nisto instar. Under these circumstances, no major discrepancy was found between larval morphological development as described here and that noted by Barnett *et al.* (1984) and Ito (1988) for those corresponding stages available to them. However, phyllosomal instar growth rates differed depending on food conditions. When larvae were fed on frozen gonad of *P. canaliculus* or frozen flesh of *D. brazieri,* they developed poorly even when nauplii of *Artemia* were given, and an extra (fifth) instar resulted. Consequently, stage III involved two instars. This phenomenon was also noted by Kneipp (1974, cited in Barnett *et al.,* 1984), when he reared newly hatched phyllosomas of *T. orientalis* in the laboratory. When development is prolonged by inferior diet, at least one extra instar can be inserted into one single stage during the sequence of phyllosomal development.

Supernumerary stages in development are well known in other lobster life histories. Marmovic *et al.* (1994) stated that under suboptimal conditions the number of ecdyses in *Ibacus peronii* increased, with smaller growth rates between molts. Many studies concerning morphological development of phyllosomas have shown that there is a great deal of uncertainty in the definition of growth stage and whether it corresponds to developmental instar or to morphological stage, especially in palinurid phyllosomas which develop over a long period of time (e.g., Robertson, 1969; Inoue, 1981; Yamakawa *et al.,* 1989; Kittaka and Kimura, 1989; Minagawa, 1990).

Variability in the number of larval instars before metamorphosis in decapod crustaceans was reviewed by Gore (1985). Causes of instar variability have been attributed to temperature (Templeman, 1936; Boyd and Johnson, 1963; Ewald, 1969; Sandifer, 1973; Criales and Anger, 1986), salinity (Templeman, 1936; Robertson, 1968; Kircher, 1970; Criales and Anger, 1986), density (Kwon, 1981), food (Templeman, 1936; Broad, 1957a, b; Yatsuzuka, 1962), population density (Ewald, 1969), and season of hatching (Díaz and Costlow, 1987). However, it is not known whether the variability reported in these studies originated from decreased metabolic levels, decreased feeding frequencies, or other factors.

Recently, Minagawa (1993) reported that differences in rearing conditions, such as temperature, salinity, density, and photoperiod affected food consumption rate in zoeas of the spanner crab *Ranina ranina* (Linnaeus). He concluded that suboptimal environmental conditions decreased feeding frequency of zoeas with consequent insufficient energy uptake resulting in slow growth and instar variability. A similar situation may explain the variability in number of instars found in phyllosomas of *T. orientalis* and *Thenus* sp. When the food of these phyllosomas has inadequate nutritional value, such as in frozen foods, they are unable to accumulate sufficient reserves for growth. As a result, the phyllosomas grow poorly, have longer instar durations, reduced molt increment in body size, and minor morphological changes. Under such conditions extra phyllosomal instar(s) may occur before metamorphosis to the nisto stage. There may also be the possibility that phyllosomas can molt without a recognizable change in morphology within the same "stage," depending on nutritional and environmental conditions surrounding the larvae. Thus, depending on prevailing trophic conditions in the plankton, phyllosomas obtained from plankton samples may have undergone an unknown number of supernumerary molts within some stage of larval development.

Morphological Differences in the Phyllosomal and Nisto Stages of *T. orientalis* Compared with *Thenus* sp.

When phyllosomas of *T. orientalis* and *Thenus* sp. were fed on fresh flesh of *D. brazieri,* they showed similar morphological development. However, there were statistical distinctions between the two species of phyllosomas in terms of: total body length of phyllosomas in each instar, including newly hatched phyllosomas (*T. orientalis* > *Thenus* sp.); the number of exopodal setae on each of the pereiopods (except on the fourth pereiopod in the first instar). Similar differences had been previously noted by Ito (1988). Ito (1988) concluded that these differences were sufficient to identify the two species of phyllosomas. However, comparisons of body size and the number of exopodal setae are not possible when rearing conditions, especially diet, differ. Since individuals of the same instar in the present study often varied in size and morphological development when fed different foods, useful comparisons between the two species can be made only between phyllosomas fed the same diet.

Although Ito (1988) directly compared laboratory-reared second instar phyllosomas of the two species, there are a number of inconsistencies in his description of morphological differences due to comparisons being made of larvae reared under inadequate conditions. The present study shows that only one character is sufficiently consistent to distinguish the two species: a short strong terminal spine (*T. orientalis*) versus short setae (one seta in first instar) (*Thenus* sp.) on the anterolateral margin of the antennule. Other differences noted by Ito (1988), including the shape of the lateral margin of the fifth pereiopod bud, the shape of the uropod buds, and the number of pairs of exopodal setae on the first to fourth pereiopods, are not consistent enough for distinguishing the two species.

ACKNOWLEDGEMENTS

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