J. Zool., Lond. (1971) **165**, 27–51

Decapod Crustacea from the International Indian Ocean Expedition
The species of *Thalassocaris* (Caridea) and their larvae

P. GOPALA MENON

Indian Ocean Biological Centre, P.O. Box 1913, Cochin, India

AND

D. I. WILLIAMSON

Marine Biological Station, Port Erin, Isle of Man

(*Accepted 9 February 1971*)

(With 13 figures in the text)

Plankton collections from the Indian Ocean contain adults and larvae of three species of *Thalassocaris: T. lucida* (Dana), *T. crinita* (Dana) and *T. obscura* **sp.n.** The new species was previously confused with *T. crinita* by Borradaile and with *T. lucida* by Kemp.

Larvae of *Thalassocaris* are described for the first time. In each species there are 10–13 zoeal stages. The cephalothorax is very broad and shallow, the maxilla has only one coxal endite, and exopods develop on legs 1–4.

T. crinita is a shallow-water species with a wide distribution in the Indian Ocean and western Pacific. *T. lucida* and *T. obscura* are open ocean species. *T. lucida* is most common in the eastern Indian Ocean (and probably in the western Pacific) and is not recorded from the Arabian Sea. *T. obscura* is most common in the Arabian Sea and is not recorded from the south-eastern Indian Ocean or from the Pacific.

Larval characters do not support the inclusion of *Thalassocaris* in the Pandalidae. Recognition of the family Thalassocarididae, comprising the genera *Thalassocaris* and *Chlorotocoides*, is advocated.

Contents

Introduction

Thalassocaris Stimpson is the most common and widespread genus of caridean crustaceans collected by the International Indian Ocean Expedition (I.I.O.E.); larvae or adults or both occur in 405 of the 1927 plankton samples taken. The genus is confined to the Indo-West Pacific Area, and this large and valuable collection of material, taken over the

greater part of the generic range, is here used as the basis for a review of the genus. The present work attempts to settle the controversial question of the number of valid species of *Thalassocaris*, and larvae of the genus are identified with certainty for the first time and described. The revised taxonomy at specific level necessitates a revision of specific distributions, and larval characters provide a new and important factor in re-assessing the taxonomic position of the genus.

The species as adults

The length of the rostrum is measured from the tip to the posterior margin of the orbit; the carapace length (c.l.) from the posterior margin of the orbit to the mid-dorsal point of the posterior carapace margin.

Thalassocaris Stimpson, 1860

Regulus Dana, 1852, *U.S. Explor. Exped.* **13,** Crust.: 597. Gender: masculine. Invalid junior homonym of *Regulus* Cuvier, 1800, *Leçons Anat. comp.* **I:** tab. 2 (Aves) (fide Holthuis, 1955). Type species, selected by Kingsley, 1880, *Proc. Acad. nat. Sci. Philad.* **1879:** 426: *Thalassiocaris lucidus* (Dana) = *Regulus lucidus* Dana, 1852, *U.S. Explor. Exped.* **13,** Crust.: 598.

Regulus Dana, 1854, *Proc. Acad. nat. Sci. Philad.* **6** (for 1852): 18, 27.

Thalassocaris Stimpson, 1860, *Proc. Acad. nat. Sci. Philad.* **1860:** 42. Gender: feminine. Substitute name for *Regulus* Dana, 1852.

Thalassiocaris Stimpson: Kingsley, 1880, *Proc. Acad. nat. Sci. Philad.* **1879:** 426. Gender: masculine. Invalid emendation and change of gender of *Thalassocaris* Stimpson, 1860.

Description

Rostrum with dorsal and ventral teeth; carapace with supra-orbital spine and two spines on anterior margin, ventral to orbit. Abdominal pleura pointed, except on anterior somites in some mature females; prominent median backwardly-directed spine on posterior margin of third somite, none on other somites. Tip of telson not bifurcate. Outer margin of stylocerite crenate; antennal scale pointed, outer margin with spines; mandible with three-segmented palp; scaphognathite with rounded posterior lobe; first leg with propodus and dactylus fused, pointed; second legs symmetrical, with undivided carpus and stout chela; dactylus of third leg with more spines in male than in female. Exopods on maxillipeds; epipods on maxillipeds and legs 1–3; arthrobranchs on third maxilliped and legs 1–4. Two pairs of luminous organs: at base of maxilla and just behind fifth leg on each side. Endopod of first pleopod inflated and bilobed in male, reduced in female; second pleopod of male with appendix masculina; pleopods 2–5 with appendix interna. Exopod of uropod with faint diaeresis, outer margin setose and ending in two spines.

Kemp (1925) stated that there is no branchiostegal spine in this genus, but he did not name the two spines beneath the orbit. Neither of these spines migrates during development; the more dorsal first appears in zoeal stage II and occurs at the level of the antennule; the other is present from the first juvenile stage and occurs at the level of the base of the antenna. In spite of Kemp's statement, we think that they are best referred to as antennal (= antennular) and branchiostegal spines.

The photophores are very distinct in living or freshly-killed specimens (Kemp, 1925) but are rather difficult to distinguish in preserved material, except after treatment with a

clearing agent. Generally the most convenient characters for separating members of the genus from other Caridea are the form of legs 1 and 2 and the spine on the third abdominal somite.

The genus occurs throughout the Indian Ocean (including the Red Sea) to about 35°S (present work) and in the western Pacific from southern Japan to Fiji (de Man, 1920).

Seven nominal species and one variety of *Thalassocaris* have been described, but Kemp's (1925) statement that the genus contains only two valid species has been widely accepted. We have re-examined type material of *T. maldivensis* Borradaile, 1915 from the University Museum, Cambridge, and of *T. novaezealandiae* Borradaile, 1916 from the British Museum, and we agree with Kemp (1925) that the former species should be included in the genus *Chlorotocoides* Kemp and is identical with *C. spinicauda* (de Man), while, as noted by de Man (1920), *T. novaezealandiae* belongs to the genus *Chlorotocus* A. Milne Edwards. *T. stimpsoni* Bate, 1888 is based on a larval form, and both de Man (1920) and Kemp (1925) questioned whether it was correctly placed in the genus *Thalassocaris*. Kemp (1925) placed both *T. danae* Bate, 1888 and *T. affinis* Borrodaile, 1915 in the synonymy of *T. lucida* (Dana, 1852) and recognized *T. crinita* (Dana, 1852) as the only other valid species of the genus. We have been able to identify *T. stimpsoni* as a larva of *T. lucida*, and we have confirmed that *T. danae* is also a synonym of the same species. We find, however, that Borradaile (1915, 1917) based his species *T. affinis* on material of two species, while Kemp (1925) confused a different combination of two species under the name *T. lucida*. The three species of the genus which we consider valid are re-described below. It has been necessary to give a new name to the third species.

Thalassocaris lucida (Dana, 1852)

(Figs 1(a), 2, 5(a) and 6(a), (b))

Regulus lucidus Dana, 1852, *U.S. Explor. Exped.* **13,** Crust.: 598, pl. 39, fig. 5 a–q. Type material probably longer extant (Dr F. A. Chace, pers. comm.). Type locality: 30 miles off Assumption I. (= Asuncion), Ladrones (= Marianas Is.).

Regulus lucidus: Dana, 1854, *Proc. Acad. nat. Sci. Philad.* **6** (for 1852): 27.

Thalassocaris lucida (Dana): Stimpson, 1860, *Proc. Acad. nat. Sci. Philad.* **1860:** 42. [*Non* Calman, 1909, *Proc. zool. Soc. Lond.* **1909:** 706. *Non* Kemp, 1925, *Rec. Indian Mus.* **27:** 283.]

Thalassiocaris lucidus (Dana): Kingsley, 1880, *Proc. Acad. nat. Sci. Philad.* **1879:** 426.

Thalassocaris fucida (Dana): Bate, 1888, *Rep. Voy. Challenger,* Zool. **24:** 683.

Thalassocaris danae Bate, 1888, *Rep. Voy. Challenger,* Zool. **24:** 683, pl. 117, fig. 1 a–c. Holotype: British Museum (Natural History), London, England. Type locality: Fiji.

Thalassocaris stimpsoni Bate, 1888, *Rep. Voy. Challenger,* Zool. **24:** 684, pl. 117, fig. 2. Holotype: British Museum (Natural History), London, England. Type locality: near Yokohama, Japan.

Material examined

I.I.O.E. (excluding larvae): 1♂ (c.l. 3·0 mm), 2 ovig. ♀♀ (c.l. 3·0, 3·2 mm), 2 juvs. (c.l. 2·4, 2·6 mm) from between Northwest Cape, Australia, and Java, within limits 9–20° S, 106–113° E; 1 juv. (c.l. 2·0 mm) off C. Comarin, India, 7° 39′ N, 78° 09′ E.

British Museum (Natural History), London, England: 1 megalopa (c.l. 2·0 mm), holotype of *T. danae* Bate, from Fiji; 1 juv. (c.l. 2·6 mm), det. Gurney as *T. danae*, from off Port Elizabeth, South Africa, 34° 30′ S, 26° 19′ E; 1 last zoeal stage, holotype of *T. stimpsoni* Bate, from near Yokohama, Japan.

Description

Rostrum almost straight or curving upwards distally; length 1·4–1·9 times that of carapace, four to six times distance between supra-orbital spines; rostrum more slender in lateral view and teeth smaller than in other species of genus; teeth 7–10/2–4; width of

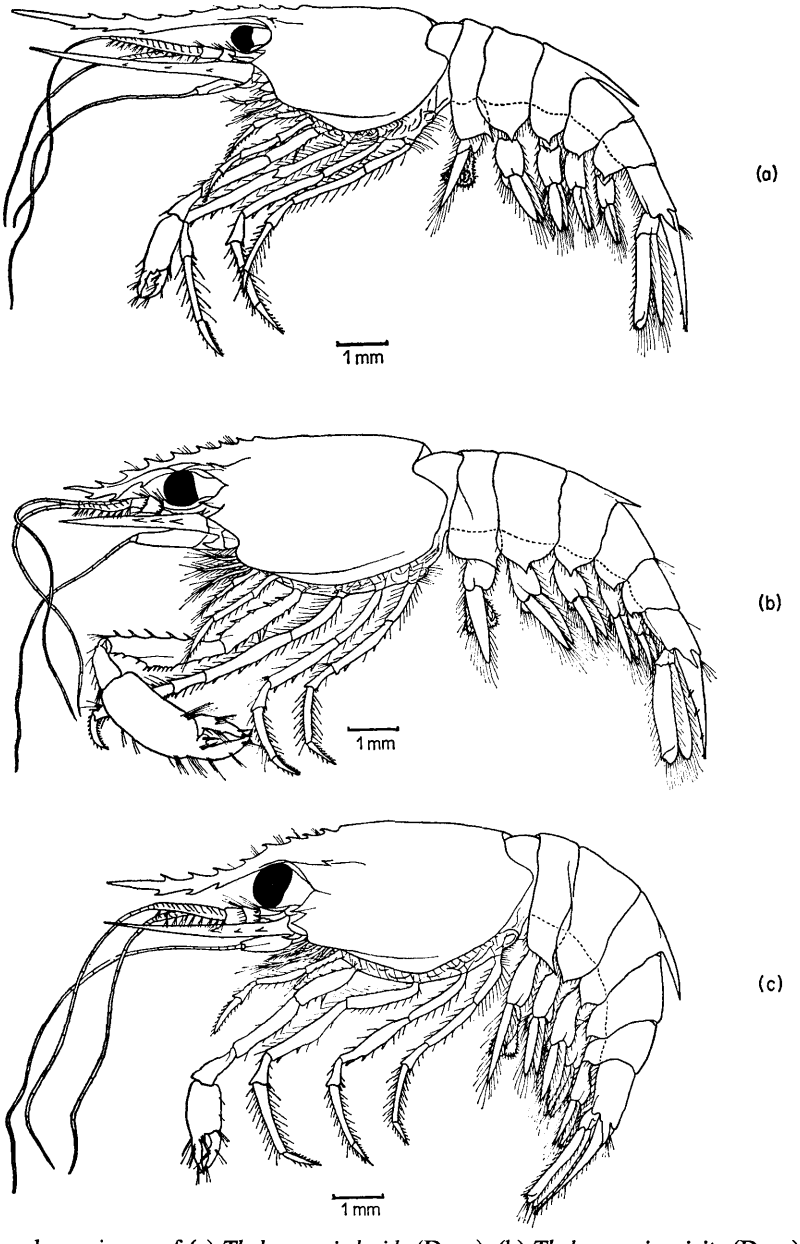

FIG. 1. Adult male specimens of (a) *Thalassocaris lucida* (Dana), (b) *Thalassocaris crinita* (Dana), (c) *Thalassocaris obscura* **sp.n.**—holotype.

rostrum decreasing only slightly from bases of supra-orbital spines, then parallel-sided between eyes; parallel portion reaching to about level of fronts of eyes in mature specimens, much shorter in juveniles, giving way to tapering portion; central and distal portions slender, often approximately parallel-sided to near tip. Supra-orbital spine small. Dorsal spine on third abdominal somite extending well beyond middle of fourth somite, sometimes to posterior border. Telson four to five times as long as maximum width, about four times as wide anteriorly as posteriorly; three (rarely four) pairs dorso-lateral spines (including pair at posterior end of lateral margin): anterior pair in anterior third of telson, second pair larger; two pairs dorsal setae near anterior end of telson; posterior margin with one pair large spines and smaller pear-shaped central spine.

Antennal scale six or seven times as long as maximum breadth, not reaching quite as far as tip of rostrum; outer margin with three (occasionally two or four) spines all in proximal half, crenate between and beyond spines. Second leg not reaching as far as tip of antennal scale; ischium with one spine; merus with few spinules; carpus smooth; propodus more than three times as long as broad, with rather small protuberance at base of fixed finger, facing dactylus; dactylus about three times as long as maximum breadth, bifurcate at tip. Dactylus of third leg of female with about seven spines on posterior face, that of male with about 17 spines.

Remarks

The length of the rostrum (appreciably longer than the carapace), its shape in dorsal view (particularly the parallel-sided portion between the eyes) and the presence of a central spine on the posterior margin of the telson provide the best means of identifying this species from other members of the genus.

The female of length nine lines (about 19 mm), drawn by Dana (1852), had a c.l. of about 3·5 mm, which is slightly larger than any of our specimens. The rostrum curved upwards more than in any of our mature specimens, but on all other points which he described or illustrated there is very good agreement.

The holotype of *T. danae* Bate appears to be a megalopa (i.e. in the first post-zoeal stage). The second spine on the carapace margin beneath the orbit is not yet developed, and there are vestiges of exopods on legs 1–4. Bate (1888) drew large setose exopods on legs 1 and 2, but this is an error. The specimen has four pairs of dorso-lateral telson spines, as opposed to three pairs in the juveniles and adults we have examined. We have, however, seen several specimens in the last zoeal stage with the additional pair of spines, and their occurrence in the megalopa may not be uncommon. Apart from the points mentioned, Bate's specimen resembles a juvenile of *T. lucida*. The specimen identified by Gurney as *T. danae* is that illustrated in Gurney & Lebour (1941). It is morphologically indistinguishable from juveniles of *T. lucida* from the I.I.O.E. collections, and it represents the most south-westerly record of that species.

The holotype of *T. stimpsoni* Bate is a specimen of *T. lucida* in the last zoeal stage (see section "The species as larvae", below). Bate (1888) did not mention that it was a larva and gave no reasons for placing it in the genus *Thalassocaris*. Both de Man (1920) and Kemp (1925) questioned its generic placing.

Material of *Thalassocaris* from two regions of the Indian Ocean was referred by Kemp (1925) to *T. lucida*. The specimens from Christmas I. which he re-examined had earlier been recorded as *T. lucida* by Calman (1909), and those from the Maldive Is. had been

used by Borradaile (1915, 1917) as some of the type material for his species *T. affinis*. We have not seen the material from Christmas I., but we find that Borradaile's specimens of *T. affinis* include two species, neither of which is *T. lucida* and nearly all of which belong to the species described below as new. (See also under the two following species, below.) It appears that the description of "*T. lucida*" given by Kemp (1925) was based on specimens of this new species, and his attempts to explain away discrepancies between his specimens and Dana's (1852) figures suggest that he had probably never seen specimens of *T. lucida* (Dana). On this assumption, we consider that the material from Christmas I. should also be referred to the new species.

The distribution of the species is discussed in a later section.

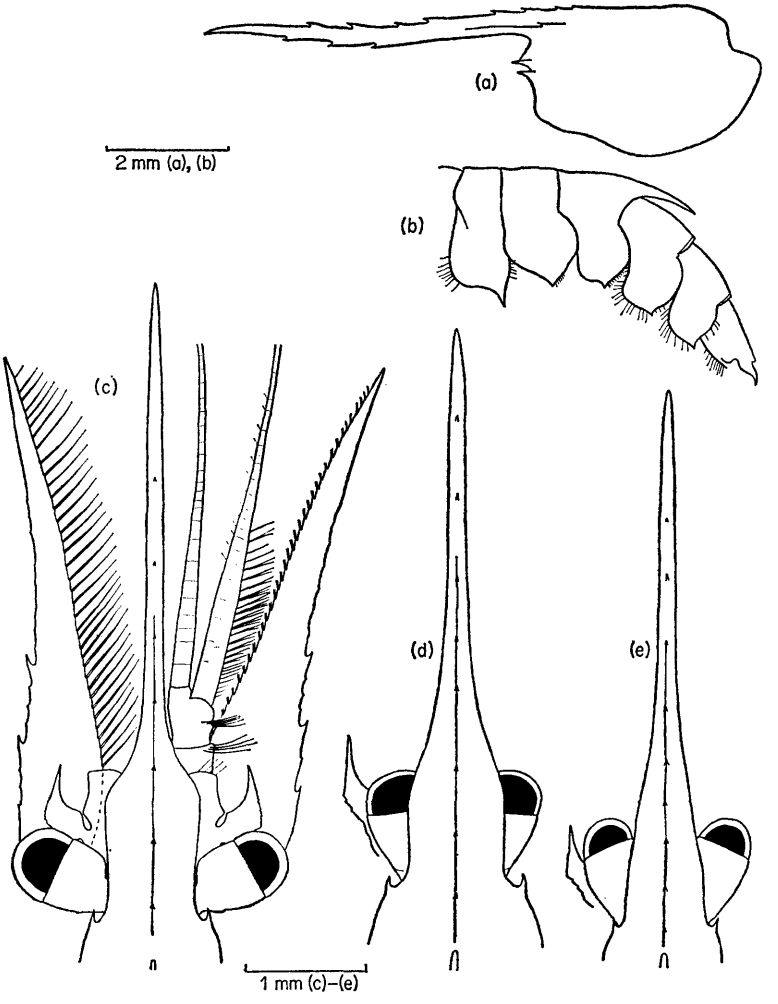

FIG. 2. *Thalassocaris lucida* (Dana): (a) carapace and rostrum of adult male (c.l. 3·0 mm), lateral; (b) abdominal somites of same, lateral; (c) head of same, dorsal; (d) rostrum etc. of ovigerous female (c.l. 3·2 mm), dorsal; (e) rostrum etc. of young male (c.l. 2·5 mm), dorsal.

Thalassocaris crinita (Dana, 1852)

(Figs 1(b), 3, 5(b) and 6(c),(d))

Regulus crinitus Dana, 1852, *U.S. Explor. Exped.* **13,** Crust.: 599, pl. 39, fig. 6 a–h. Type material probably no longer extant (Dr F. A. Chace, pers. comm.). Type locality: Sooloo Sea.

Regulus crinitus: Dana, 1854, *Proc. Acad. nat. Sci. Philad.* **6** for (1852): 27.

Thalassocaris crinitus (Dana): Balss, 1914, *Abh. bayer. Akad. Wiss.* (Suppl.) **2**(10): 28.

Thalassocaris affinis Borradaile (partim), 1915, *Ann. Mag. nat. Hist.* (8) **15:** 208. Syntypes: University Museum of Zoology, Cambridge, England (Gardiner Coll., Ref. 20 June, 1900). Type locality: Maldive Is. and Saya de Malha. Lectotype: see below.

Thalassocaris crinita (Dana): de Man, 1920, *Siboga Exped.* **39a3:** 95, pl. 9, figs 22–22o.

Thalassocaris crinita (Dana) var.?: de Man, 1920, *Siboga Exped.* **39a3:** 100, pl. 10, figs 23–23c.

Thalassocaris crinita (Dana) subsp?: Zarenkov, 1968, *Byull. mosk. Obshch. Ispyt. Prir.*, Biol. **73**(3): 58.

Thalassocaris NRS 7: Williamson, 1970, Bull. Sea Fish. Res. Stn, Haifa No. 56: 13, fig. 9.

Material examined

I.I.O.E. (excluding larvae): 1♂ (c.l. 4·3 mm), 14 juvs. (c.l. 1·8–2·5 mm) from coast of north-west India, 20° 00′ N 70° 17′ E.

University Museum of Zoology, Cambridge, England: 1♂ (c.l. 5·0 mm), syntype of *T. affinis* Borradaile, from Mahlos Atoll, Maldive Is.; 1 ovig. ♀ (c.l. 3·0 mm), det. Borradaile as *T. affinis*, from Saya de Malha Bank; 4♂♂ (c.l. 4·2–5·1 mm), 4♀♀ (c.l. 3·5–6·8 mm), det. Borradaile as *T. crinitus*, from Maldive Is., Amirante Is., Seychelle Is., Saya de Malha Bank and Cargados Carajos.

Description

Rostrum deep with conspicuous dorsal crest, curving downwards from base, horizontal near tip; length 0·7–1·2 times that of carapace, 2·0–2·5 times distance between supra-orbital spines; teeth larger than in other species of genus, 7–10/2–3; rostrum of mature specimens widest at level of fronts of eyes, then narrowing rapidly; rostrum of juveniles parallel-sided between eyes. Supra-orbital spine large. Dorsal spine on third abdominal somite extending to $\frac{1}{4}$–$\frac{3}{4}$ length of fourth somite. Telson 2·5–3·0 times as long as maximum width, four or five times as wide anteriorly as posteriorly; two pairs long dorsal setae near anterior end; four pairs dorso-lateral spines (including pair at end of lateral margin), anterior pair near middle of length of telson; posterior margin with pair of large spines and much smaller central spine.

Antennal scale four or five times as long as maximum breadth, reaching to tip of rostrum or slightly beyond; outer margin with three large spines, distal spine usually just in distal half of scale; margin smooth between spines and smooth or slightly crenulate beyond. Second leg reaching well beyond rostrum; merus of large specimens usually with conspicuous tubercles and spines but occasionally with small tubercles and few spines or almost smooth; merus of small specimens without tubercles; propodus (including finger) about twice as long as broad; mature specimens with large protuberance and deep indentation on fixed finger, facing dactylus; propodus and dactylus with many tufts of stiff setae. Dactylus of third leg with about seven spines on posterior face in female, larger and with about 18 spines in male.

Remarks

In large specimens, the shape of the rostrum in dorsal view is very characteristic, and the specimens from the Indian Ocean are in very good agreement with that illustrated by Dana (1852). In small specimens the base of the rostrum is parallel-sided, somewhat resembling the condition in mature specimens of *T. lucida*; the rostrum is, however, always shorter in the present species, and the stout rostral spines and large chela provide other convenient points of distinction.

The variable form of the merus of the second leg of *T. crinita* has led to considerable confusion. We find that in juveniles it is always devoid of tubercles although it may bear a

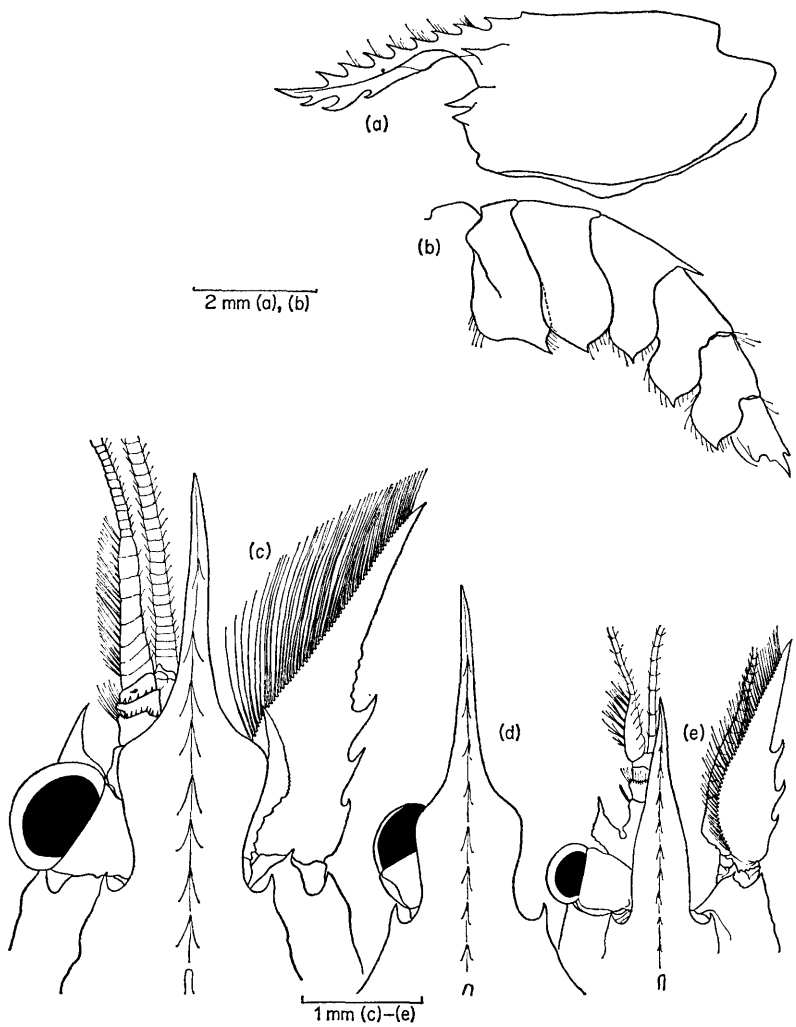

FIG. 3. *Thalassocaris crinita* (Dana): (a) carapace and rostrum of adult male (c.l. 4·3 mm), lateral; (b) abdominal somites of same, lateral; (c) head of same, dorsal; (d) rostrum etc. of young female (c.l. 3·0 mm), dorsal; (e) rostrum etc. of juvenile (c.l. 2·1 mm), dorsal.

few spines. In mature specimens the condition may range from smooth to conspicuously tuberculate with large spines, and there is considerable overlap in size between "smooth" and "tuberculate" specimens. The collection in the Cambridge Museum contains several specimens in intermediate conditions, in which the tubercles and spines are poorly developed or confined to the proximal end of the merus, and smooth and tuberculate specimens have been taken from the same area. Specimens differing in the armature of the second leg show no other consistent differences, and we do not think that any valid taxonomic distinction can be made on this basis, even at an infra-specific level.

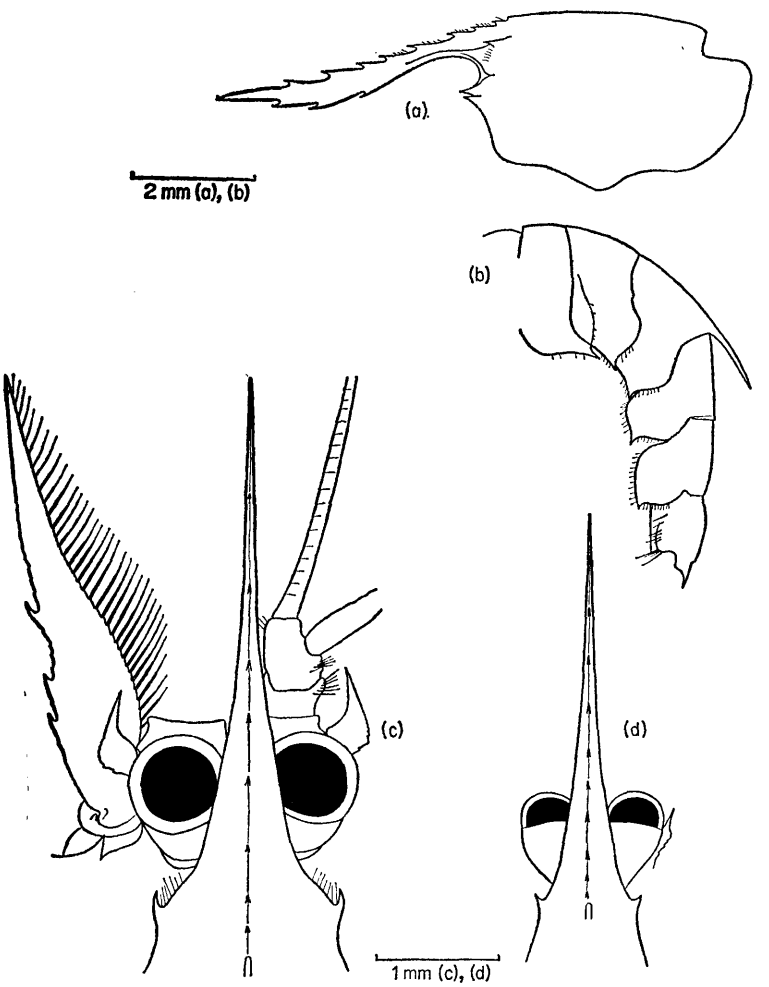

FIG. 4. *Thalassocaris obscura* **sp.n.:** (a) carapace and rostrum of adult male (holotype: c.l. 3·6 mm), lateral; (b) abdominal somites of same, lateral; (c) head of same, dorsal; (d) rostrum etc. of juvenile (c.l. 1·9 mm), dorsal.

Dana (1852) neither drew nor mentioned tubercles on the merus of the second leg of *Regulus crinitus*, and it is possible that this joint was smooth in his type specimen. Those specimens from the western Indian Ocean which Borradaile (1917) identified as *T. crinitus* (*sic*) all have the merus more or less tuberculate, but the same collection also contains two

specimens, which we unhesitatingly refer to *T. crinita*, in which the merus is practically smooth. These two, a male (c.l. 5·0 mm) from the Maldive Is. and an ovigerous female (c.l. 3·0 mm) from Saya de Malha Bank, were referred by Borradaile to his new species *T. affinis*, together with 20 specimens of the species we describe below. It is notable that while Borradaile (1915, 1917) regarded *T. affinis* as being intermediate between *T. lucida* and *T. crinita*, he gave no characters whereby his species might be distinguished from *T. crinita*. Although the majority of the syntypes of *T. affinis* Borradaile, 1915 belong to what was indeed a new species, the only figure to be published under this name (Borradaile, 1917, pl. 58, fig. 4) is of the male specimen of *T. crinita* to which we have just referred. There is very good agreement between the drawing and the specimen, and it is the only specimen in this collection in which the rostrum is shorter than the carapace. The confusion over the use of the name *Thalassocaris affinis* Borradaile can only be resolved by the designation of a lectotype, and we have followed Recommendation 74B of the International Code of Zoological Nomenclature in selecting the specimen figured by Borradaile:

Thalassocaris affinis Borradaile, 1915. Lectotype, by present selection: ♂, c.l. 5·0 mm, from Mahlos Atoll, Maldive Is., coll. J. S. Gardiner. Now separated from seven other syntypes from same locality. (University Museum of Zoology, Cambridge, England. Gardiner Coll. Reg. 20 June 1900.)

This action makes the name *T. affinis* Borradaile a junior subjective synonym of *T. crinita* (Dana).

De Man (1920) suggested that those specimens in which the merus of the second leg remains smooth should be recognized as a variety of *T. crinita*, and Zarenkov (1968) recorded such specimens as "subsp.?". Both regarded the form in which the merus is tuberculate ("of uncouth appearance": de Man) as corresponding to the type material, although there appears to be no evidence to support this view. We have given our reasons for considering that the species should not be sub-divided on the form of the merus of the second leg.

The two specimens from the northern Red Sea, a male of c.l. 4·0 mm and a last zoea, described by Williamson (1970), can now be confidently referred to *T. crinita*.

The distribution of this species is discussed in a later section.

Thalassocaris obscura sp. n.

(Figs 1(c), 4, 5(c) and 6(e))

Holotype: ♂. c.l. 3·6 mm, coll. R.V. "Varuna", stn. 2007, 15.10 h (local) 4.xi.1963, Arabian Sea 09° 00′ N, 75° 20′ E, plankton 200–0 m, sounding 2100 m. British Museum (Nat. Hist.), London, England, Reg. No. 1970; 207.

Paratype: ♀, c.l. 3·7 mm, collection details as for holotype. Indian Ocean Biological Centre, Cochin, India.

Thalassocaris affinis Borradaile (partim) 1915, *Ann. Mag. nat. Hist.* (8) **15:** 208. Type material: see under *T. crinita*.

Thalassocaris lucida: Calman, 1909, *Proc. zool. Soc. Lond.* **1909:** 706. Kemp, 1925, *Rec. Indian Mus.* **27:** 283 George & George, 1964, *J. mar. biol. Ass. India* **6:** 171.

[*Non Regulus lucidus* Dana, 1852, *U.S. Explor. Exped.* **13,** Crust.: 598, pl. 39, fig. 5 a–q.]

Material examined

I.I.O.E. (excluding larvae): more than 200 ♂♂, ♀♀ and juvs. (c.l. 1·7–4·25 mm), mostly from Arabian Sea and Bay of Bengal.

University Museum of Zoology, Cambridge, England: 20 ♂♂ and ♀♀ (c.l. 3·0–4·7 mm),

from Maldive Is., paralectotypes and paratypes of *Thalassocaris affinis* Borradaile, 1915. (For designation of lectotype of *T. affinis*, see under previous species.)

Description

Rostrum sloping downwards in front of eyes, then horizontal; length 1·1–2·0 times that of carapace (less than 1·5 times carapace where c.l. exceeds 3 mm); length three or four times distance between supra-orbital spines; teeth rather smaller than in *T. crinita*, 7–11/2–4; width of rostrum decreasing rapidly near base in large specimens, more gradually in juveniles, then tapering fairly evenly from level of bases of eyes to tip. Supra-orbital spines intermediate in size between those of other two species. Spine on posterior margin of third somite overlapping two-thirds or more of fourth somite. Telson almost four times as long as maximum width, five or six times as wide anteriorly as posteriorly; three pairs dorsal setae near anterior end; three pairs sub-equal dorso-lateral spines, anterior pair in anterior one-third of telson, posterior pair overlapping pair of long spines on posterior margin; pair of setae between long posterior spines but no median spine.

Antennal scale five to seven times as long as maximum breadth, reaching to about same

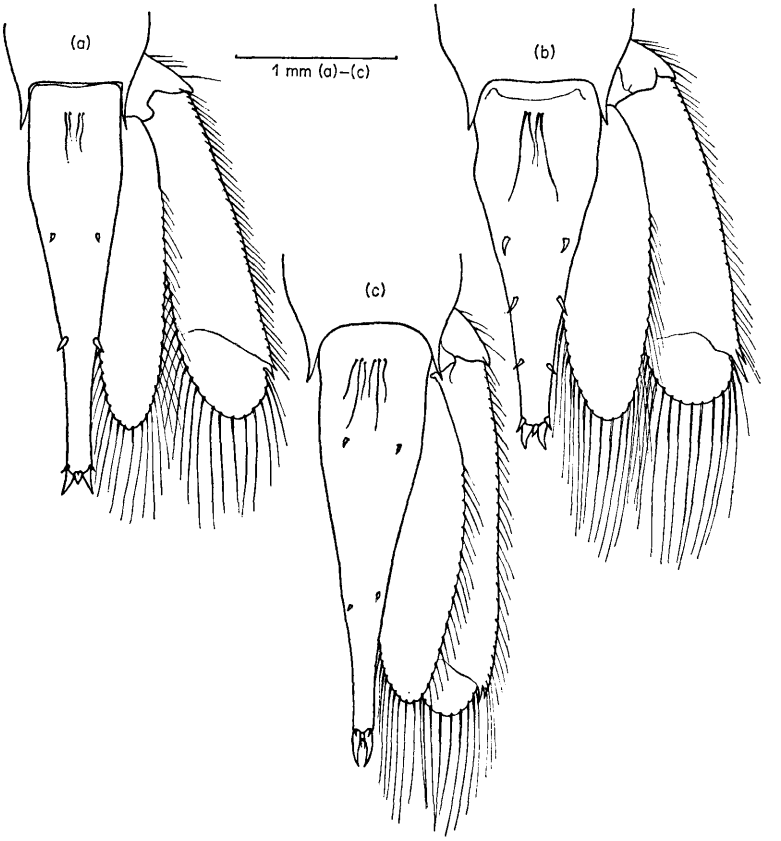

FIG. 5. Telson and right uropod: (a) *Thalassocaris lucida* (Dana), male, c.l. 3·0 mm. (b) *Thalassocaris crinita* (Dana), male, c.l. 4·3 mm. (c) *Thalassocaris obscura* **sp. n.**: male, c.l. 3·6 mm (holotype).

level as tip of rostrum; outer margin with (2)3(4) prominent spines, not uncommonly with different number on left and right; distal spine the largest, situated in middle of margin or just in proximal half; margin crenate between spines and for short distance beyond distal spine. Merus of second leg with small ventral spinules, never tuberculate; propodus slightly less than three times as long as broad, protuberance at base of fixed finger intermediate in size between those of other two species. Dactylus of third leg showing little sexual dimorphism: seven to nine spines on posterior face in female, 10–12 in male.

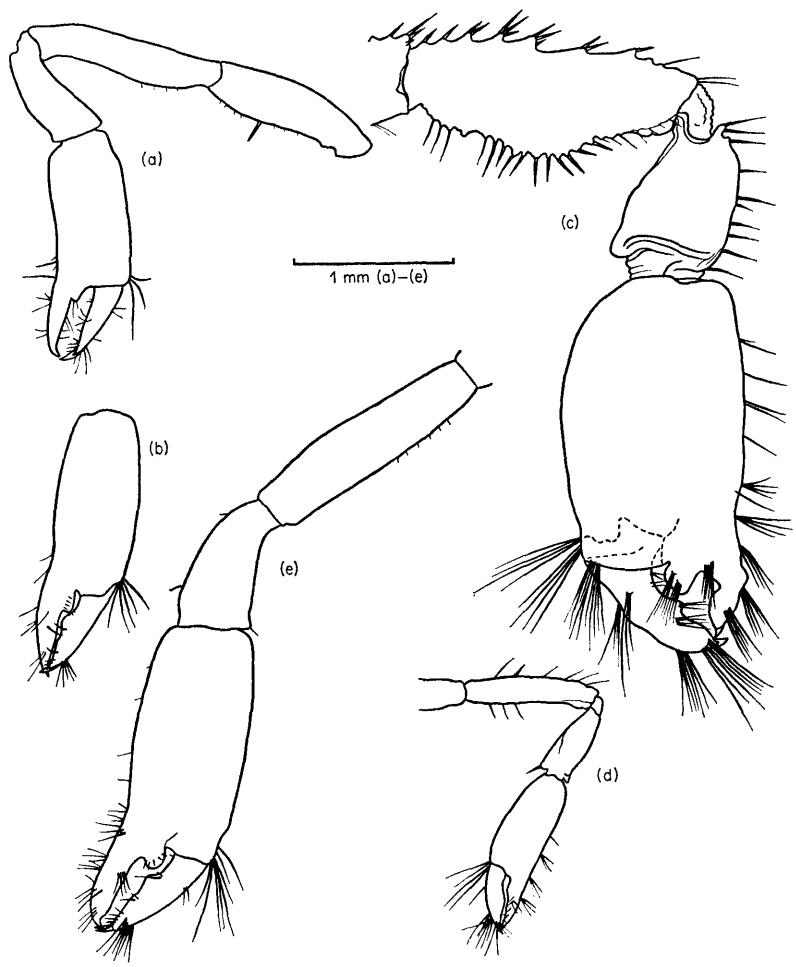

FIG. 6. Second leg. (a), (b) *Thalassocaris lucida* (Dana): (a) male, c.l. 3·0 mm; (b) ovigerous female, c.l. 3·2 mm. (c), (d) *Thalassocaris crinita* (Dana): (c) male, c.l. 4·3 mm; (d) juvenile, c.l. 2·1 mm. (e) *Thalassocaris obscura* **sp. n** ovigerous female, c.l. 4·25 mm.

Remarks

Many of the characters of *T. obscura* are intermediate between those of *T. lucida* and *T. crinita*, but not the shape of the rostrum in dorsal view, the lack of a central telson spine and the poorly developed sexual dimorphism of the dactylus of the third leg.

Borradaile (1915, 1917) had at his disposal material containing *T. crinita* and the present species. He appears to have separated it into two species purely on the form of the merus of the second leg, regarding those specimens with a tuberculate merus as belonging to *T. crinitus* (*sic*) and creating his species *T. affinis* for those with a smooth merus. We have already shown that this character is very variable in *T. crinita*, and we find that Borradaile's material of *T. affinis* from the Maldive Is. contains one specimen of *T. crinita* and 20 specimens of *T. obscura* (see also under *T. crinita*). Kemp (1925), on re-examining Borradaile's material, apparently missed the specimen of *T. crinita* and mis-identified the specimens of *T. obscura* as *T. lucida*. Kemp (1925) also re-examined specimens from Christmas I., Indian Ocean, and agreed with Calman (1909) in assigning them to *T. lucida*. We have not been able to trace these specimens, but, as Kemp found them in good agreement with those from the Maldive Is., we suggest that they too should be referred to *T. obscura*. The specimens from the Red Sea and the Maldive Is. recorded by Calman (1939) also seem likely to have been *T. obscura*. Dr M. J. George has kindly re-examined the material from tuna stomachs from the Arabian Sea, originally recorded as *T. lucida* by George & George (1964). Comparison with our figures of *T. lucida* and *T. obscura* shows the specimens to belong to the latter species.

The distribution of all three species is discussed in a later section.

The species as larvae

The length "carapace+rostrum" used in this section is the overall length from the tip of the rostrum to the most posterior part of the carapace. The terms "zoea" and "megalopa" are used as defined by Williamson (1969).

Williamson (1970) described a larva of *Thalassocaris*, but the identification was based on unpublished observations on I.I.O.E. material. The only other larvae which have been referred to *Thalassocaris* are those to which Bate (1888) gave the name *T. stimpsoni*. He did not mention that this species was based on larval material and gave no reasons for including it in the genus. Apart from a pointed antennal scale and a developing chela on the second leg, the specimens showed none of the characters listed by Bate in his definition of the genus, and the dorso-ventrally compressed larval carapace is in marked contrast to that of the adult. De Man (1920) regarded *T. stimpsoni* as "a larval form, probably not pertaining to this genus", while Kemp (1925) stated: "The form can never be recognized again with certainty and it is not clear that it really belongs to the genus in which it is placed."

Larvae showing only small (specific) differences from *T. stimpsoni* are very common in I.I.O.E. material, and late larvae frequently occur in the same samples as juveniles of *T. obscura*. No comparable correlation is shown between the occurrence of such larvae and that of any other decapod species. More positive evidence that the larvae and juveniles belong to the same species was obtained from the examination of specimens in the last zoeal stage which were about to moult or in the process of moulting. These showed that the following stage (megalopa) would have teeth on both the rostrum and the antennal scale corresponding to those of an adult *Thalassocaris* (e.g. Fig. 11(i)). Confirmation of the identity of the larvae was provided by several samples which yielded not only a complete or almost complete series of larval stages but also females with hatching eggs. Emerging larvae obtained from such females showed excellent agreement with free larvae in the first

zoeal stage. There is therefore overwhelming evidence that the larvae so commonly taken with juveniles and adults of *T. obscura* belong to the same species.

Adults of *T. lucida* and *T. crinita* were taken in comparatively few I.I.O.E. samples, and there was no overlapping of species. Larvae differing from those of *T. obscura* chiefly in the shape of the antennal scale occurred in several of these samples and we have assumed them to belong to the same species as the adults with which they were taken. Larvae of *T. lucida* and *T. crinita* identified on this basis differ slightly in size and in a few minor characters described below. The holotype of *T. stimpsoni* Bate, 1888, is in good agreement with Indian Ocean specimens of *T. lucida* in the last zoeal stage, and the larva described by Williamson (1970) from the northern Red Sea is a specimen of *T. crinita* in the same stage.

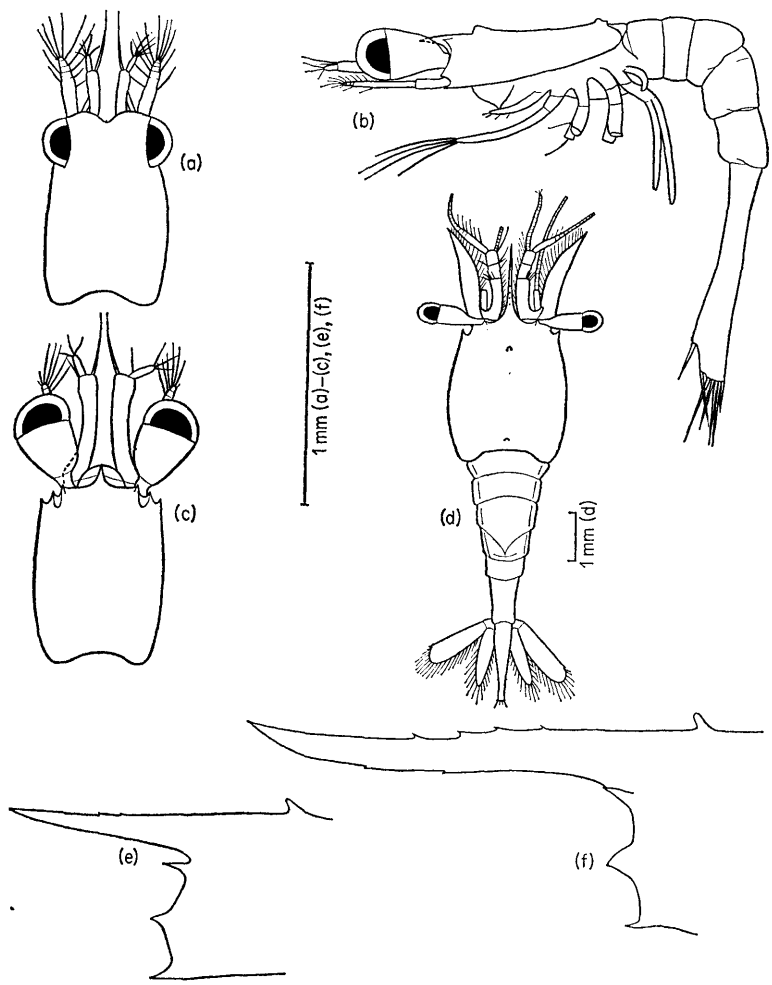

FIG. 7. *Thalassocaris obscura* **sp.n.**: larvae: (a) zoeal stage I, cephalothorax, dorsal; (b), (c) zoeal stage II: (b) lateral view; (c) cephalothorax, dorsal; (d) last zoeal stage, dorsal; (e) rostrum and anterior carapace, lateral of penultimate zoeal stage; (f) the same of last zoeal stage.

In the I.I.O.E. samples, the larvae of each species show a much wider distribution than the adults, but material for drawings and descriptions of larvae has been taken only from regions where adults were also taken.

Number of stages

For all three species, stages can be assigned with certainty only to zoeal stages I–IV. The total number of zoeal stages is probably not fixed, and consideration of the range in size of the early stages and the increase in size between them suggests that most individuals would pass through between 10 and 13 zoeal stages. For the purposes of the following descriptions, the zoeal material of each species has been divided into 11 stages, but while this probably represents fairly typical development, we would stress that many individuals probably develop more quickly or more slowly.

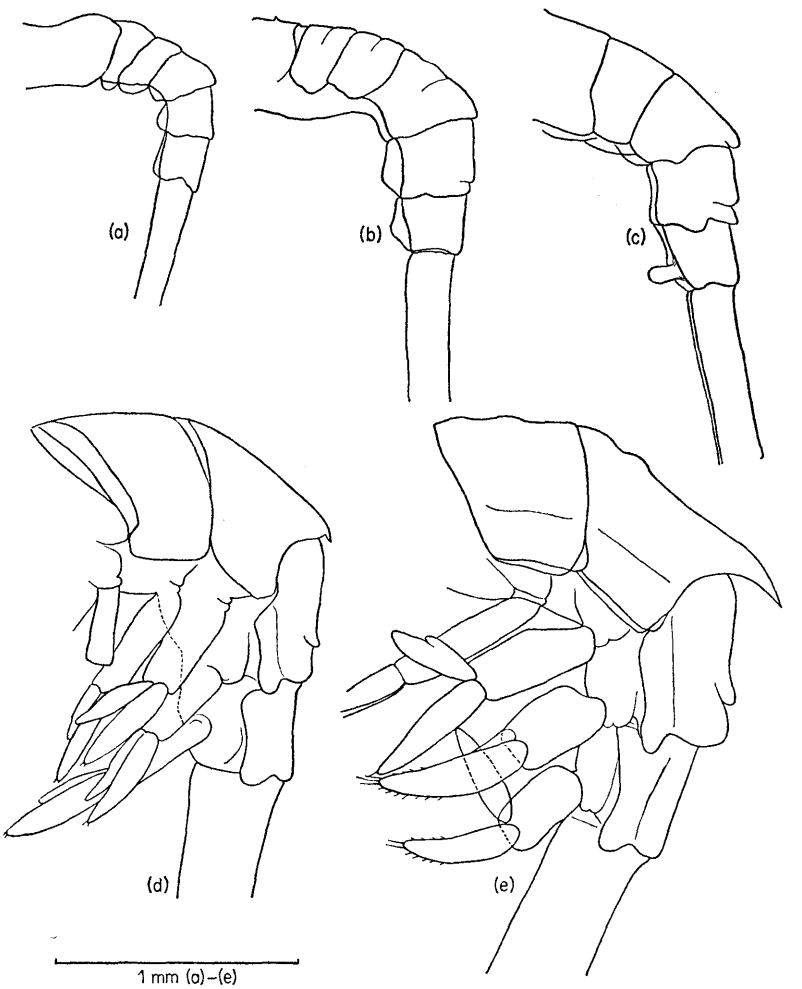

FIG. 8. *Thalassocaris obscura* **sp.n.**: larvae: (a)–(e) lateral view of part of abdomen in zoeal stages II, IV, V, X and XI (=last).

A few specimens have been taken in the megalopa stage (= post-larva *sensu* Gurney, 1942). These resemble juveniles apart from the absence of a branchiostegal spine on the carapace and the presence of vestiges of exopods on legs 1–4. There is probably only one such stage between the last zoea and the first juvenile stage.

Description (Figs 7–12)

Larval material of *T. obscura* is much more abundant in the I.I.O.E. collections than that of either of the other species of the genus, and early stages of *T. lucida* are not represented. Figures of larvae of *T. lucida* and *T. crinita* are included only to illustrate characters where differences from *T. obscura* have been noticed.

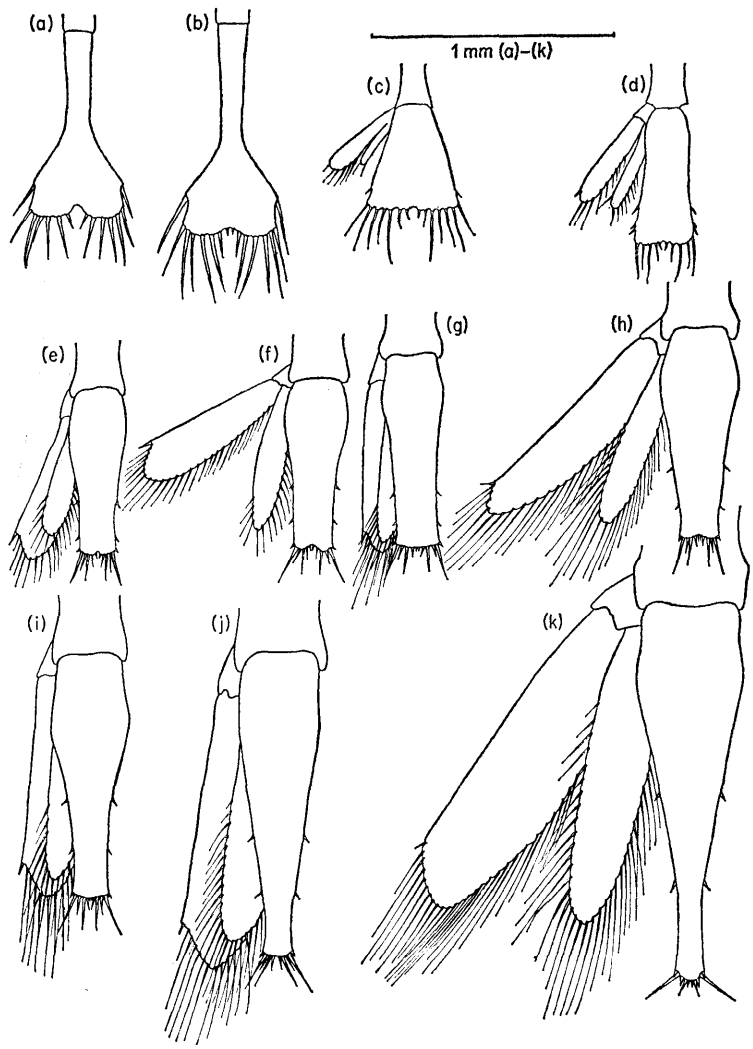

FIG. 9. *Thalassocaris obscura* **sp.n.**: larvae: (a)–(k) telson in zoeal stages I–XI.

Total length of *T. obscura* from 2·1–2·2 mm in stage I to 9·0–10·5 mm in last zoeal stage, but specimens usually bent and total length difficult to measure. Length of carapace+rostrum in each of 11 (assumed) zoeal stages approximately 0·75, 0·8, 0·9, 1·1, 1·3, 1·6, 2·0, 2·5, 3·3, 4·1 and 5·0 mm. Larvae of *T. crinita* rather smaller; total length about 1·8 mm in stage I, 8–9 mm in last zoeal stage; length of carapace+rostrum in 11 (assumed) zoeal stages 0·6, 0·7, 0·8, 1·0, 1·3, 1·6, 1·9, 2·3, 2·7, 3·1 and 3·5 mm. Early zoeal stages of *T. lucida* not obtained; later zoeal stages of similar size to comparable larvae of *T. obscura*.

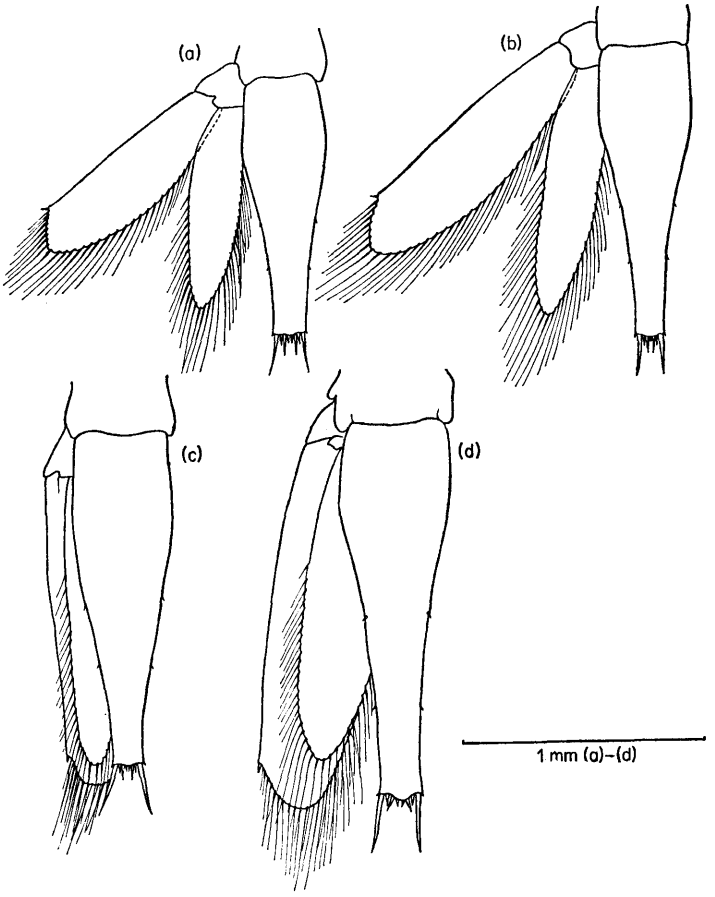

FIG. 10. Telson in penultimate and last zoeal stages: (a), (b) *Thalassocaris crinita* (Dana); (c), (d) *Thalassocaris lucida* (Dana).

Carapace (Fig. 7) broad and shallow in all zoeal stages, width about two-thirds length (excluding rostrum). Rostrum minute or absent in stage I; slightly more than one-tenth length of carapace in stage II; remaining less than one-fifth length of carapace until about stage IX; increasing to distinctly more than half length of carapace and as long as antennular peduncle in last zoeal stage of *T. obscura* and *T. lucida*, slightly less than half carapace and about three quarters length of antennular peduncle in last zoeal stage of

T. crinita; 2–3/0–1 minute teeth in stage X, 3–5/1–2 in last zoeal stage (= XI). Pterygostomian spine present in all zoeal stages, absent in megalopa and subsequent stages; supra-orbital and sub-orbital spines present from zoeal stage II but supra-orbital small and blunt in stage II; branchiostegal spine present from first juvenile stage; no denticles on ventral margin of carapace. Anterior and posterior dorsal tubercles prominent in all zoeal stages.

Abdominal somite 3 (Fig. 8) with small blunt mid-dorsal "lip" on posterior margin from stage V or VI, produced into small spine in stage X and large spine in stage XI (last

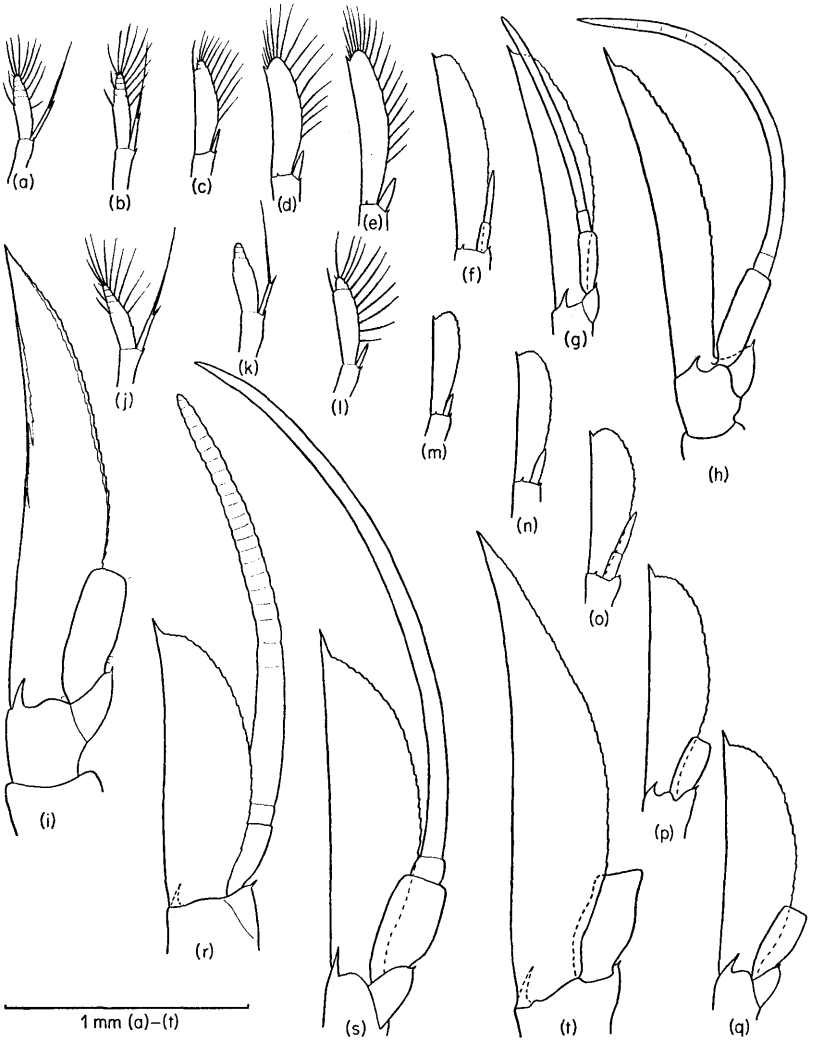

FIG. 11. Antenna in larval stages: (a)–(i) *Thalassocaris obscura* **sp. n.** in zoeal stages I–VI, VIII, X and XI (= (last); (j)–(r) *Thalassocaris crinita* (Dana) in zoeal stages I–VI, VIII, IX and XI (= last); (s), (t) *Thalassocaris lucida* (Dana) in zoeal stages X and XI (= last).

zoeal stage). Abdominal somite 4 with dorsal step at about three quarter length of somite: indistinct in stage III, distinct in all later stages, lip-like in last two zoeal stages. No other abdominal spines.

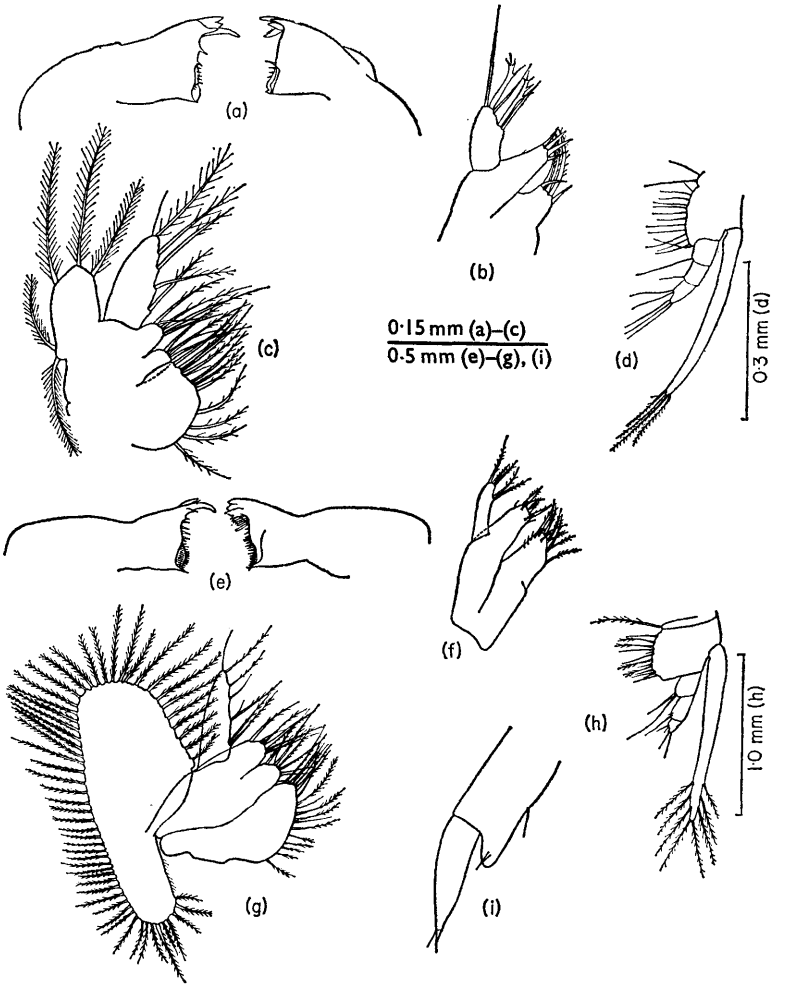

FIG. 12. *Thalassocaris obscura* **sp. n.**: larvae: (a)–(d) zoeal stage II; (e)–(i) last zoeal stage. (a), (e) Mandibles; (b), (f) maxillule; (c), (g) maxilla; (d), (h) first maxilliped; (i) end of second leg.

Telson (Figs 9 and 10) with 7+7 spines and fairly large central indentation in posterior margin in stage I, small eighth pair spines and smaller indentation in stage II. Articulation with 6th somite in stage III; posterior margin almost straight and almost as wide as length of telson; outermost pair spines on lateral margin. Slightly wider posteriorly than anteriorly in stage IV; three pairs lateral spines. Becoming progressively longer and narrower posteriorly in succeeding stages; fourth pair spines the longest, never more than twice length of sixth pair in *T. obscura*, exceeding twice length of sixth pair in last two zoeal stages of *T. crinita*, about four times sixth pair in last two zoeal stages of *T. lucida*. Lateral

spines very small in late stages of *T. crinita* and *T. lucida*, larger in *T. obscura*; additional pair spines between second and third pairs sometimes present in last zoeal stage of all species, probably more common in *T. crinita* and *T. lucida*.

Eyes stalked from stage II, longer and narrower in later stages; cornea oval. Antennules fairly widely separated at base, slightly curved; unsegmented peduncle bearing outer segment and inner seta on terminal margin in early stages, peduncle of later stages three-segmented and bearing two flagella.

Antennal protopod bearing inner spine at base of endoped from stage I and ventrally at base of exopod from stage IV (Fig. 11). Endopod ending in spine and seta in stages I and II, simple rod in stage III and following stages; basal segment formed in stage VI. Exopod (scale) segmented at tip in stages I–III; with two setae on outer margin in stages I and II, one at distal end of margin in stage III, replaced by small spine in stage IV; small tubercle on inner margin, proximal to setae, in stage I. Scale becoming progressively more pointed in later stages, with reduction in terminal lobe; tapers to point in last zoeal stage of *T. obscura* and *T. lucida* but terminal spine remains distinct in *T. crinita*. Ratio breadth: length of scale slightly greater in *T. crinita* than in *T. lucida*; considerably greater in both these species than in *T. obscura* in corresponding stage.

Mandibles asymmetrical; incisor and molar processes well separated; no palp in zoeal stages. Maxillule with unsegmented palp; no trace of exopod in any stage. Maxilla with three well-developed endites (only one on coxa); endopod broad, unsegmented; exopod broad, especially in late zoeal stages.

Maxillipeds 1–3 with setose exopods from stage I. Leg 1 a small biramous bud in stage I, other legs not represented at hatching. Exopods of legs 1 and 2 functional from stage IV; legs 1–4 with functional exopods from stage VI or VII; leg 5 without exopod in all stages. Exopods of legs 1–4 reduced and functionless in megalopa, absent in first juvenile stage.

Pleopods first appear as small buds in stage V; two small terminal setae on exopod in penultimate zoeal stage, more in last stage; fully setose in megalopa. Uropods present from zoeal stage III; unsegmented in stage III, endopod about two-thirds length of exopod, with two terminal setae, exopod without spine; rami articulate with protopod in stage IV and all later stages, endopod slightly shorter than exopod, exopod with spine at distal end of outer margin. Exopod of megalopa and juvenile stages with diaeresis and setose outer margin ending in two spines.

Larvae of *T. obscura* are most easily distinguished from those of the other two species by the comparatively narrow antennal scale. Larvae of *T. lucida* and *T. crinita* may be separated in the last two zoeal stages by the shape of the antennal scale and telson, but in earlier stages they are very similar. Those stages of *T. lucida* and *T. crinita* which could be separated with certainty (late larvae, juveniles and adults) did not occur together, *T. lucida* being confined to deep water and *T. crinita* to shallow water (see below).

Distribution

The distribution of each of the three species in I.I.O.E. material is shown in Fig. 13. This figure shows only presence or absence in each 5° square from which samples were taken. The symbols do not show the exact positions of samples and take no account of abundance or the number of samples taken in each square. All samples were taken with plankton nets, usually the Indian Ocean Standard Net, in the upper 200 m.

Only six juveniles and adults of *T. lucida* were taken, five between Java and North West Cape, Australia, and one off Cape Comarin, India. Larvae were usually taken singly, and nowhere were more than three found in any one sample. Most of the larvae assigned to *T. lucida* were in the last two zoeal stages and could be identified with certainty.

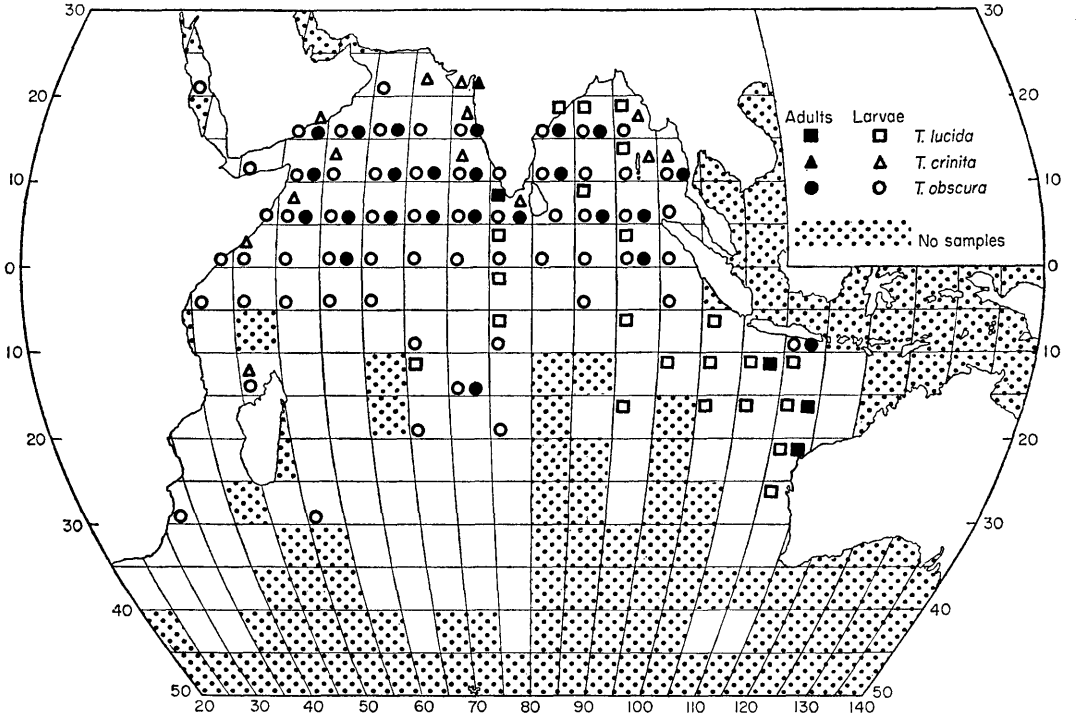

FIG. 13. Occurrence within 5° squares of *Thalassocaris lucida* (Dana), *T. crinita* (Dana) and *T. obscura* **sp. n.** in samples collected during the International Indian Ocean Expedition.

There was difficulty in deciding whether earlier larvae belonged to *T. lucida* or *T. crinita*, but such specimens were assigned to the same species as late larvae or adults occurring in the vicinity. The great majority of the records of *T. lucida* were from the eastern Indian Ocean, in a broad band stretching from the Bay of Bengal to north-west Australia, and occasional larvae were taken in the central Indian Ocean. The species was not represented in the large number of samples from the Arabian Sea, and re-examination of specimens from this region assigned to *T. lucida* by Kemp (1925) and by George & George (1964) has shown them to belong to *T. obscura*. The specimens from the Red Sea recorded by Calman (1939) should probably also be referred to *T. obscura*. Although *T. lucida* was not taken off the east African coast during the I.I.O.E., the record by Gurney (in Gurney & Lebour, 1941) from off Port Elizabeth, South Africa, is confirmed as belonging to this species. The juvenile from off Cape Comarin was taken where the sounding was only 300 m but very near the edge of the continental shelf. All other records of the species were from soundings of more than 1000 m and many from more than 4000 m. It appears to be a species of the open ocean.

Records of *T. lucida* from outside the Indian Ocean are all from the western Pacific: from off the Marianas Is. (Dana, 1852), from near Yokohama, Japan, and off Fiji (Bate, 1888).

Adults and juveniles of *T. crinita* were taken only off the coast of north-west India, in position 20° 00′ N, 70° 17′ E, in a sounding of 95 m. Larvae were fairly common (up to nine per sample) in this region, between the coast and the edge of the continental shelf. Small numbers were taken on other coasts of the Arabian Sea (coasts of southern India, Arabia and east Africa), off northern Madagascar and in the eastern part of the Bay of Bengal (coasts of Burma and Andaman Is.). Two records of larvae were from over the continental slope of north-west India, in soundings of 1250 m; all other records were from over the continental shelf, mostly in water of less than 100 m. Earlier records from the Indian Ocean include the Maldive Is., Amirante Is., Seychelle Is., Saya de Malha Bank and Cargados Carajos (Borradaile, 1917), Ceylon (Kemp, 1925) and the northern Red Sea (Williamson, 1970). The species is also recorded from the western Pacific: the Philippines and Indonesia (Dana, 1852; de Man, 1920) and Japan (Balss, 1914).

The present collection shows *T. obscura* to be the most common species of *Thalassocaris* over most of the Indian Ocean. The largest numbers were taken in the Arabian Sea, from which many samples contained more than five adults and juveniles and more than 20 larvae. Rather smaller numbers were taken in the Bay of Bengal. The species appears to be much less common south of the equator; small numbers were taken at widely separated stations in the south-western Indian Ocean, and none were recorded from the south-eastern region bounded by 10° S and 80° E. A few larvae were collected over the continental shelf of south-west India in soundings of less than 100 m, but practically all the other records (including that from the central Red Sea) were from soundings of over 1000 m. Previous records which are now referred to this species are from the Maldive Is. (Borradaile, 1917, as *T. Affinis*), Christmas I. (Calman, 1919, as *T. lucida*) and the Red Sea (Calman, 1939, as *T. lucida*). There are no records of *T. obscura* from outside the Indian Ocean (including the Red Sea).

The general picture of distribution which emerges is that *T. crinita* is a shallow-water species from localities scattered throughout the Indian Ocean and extending into the western Pacific. *T. lucida* and *T. obscura* are both species associated with deep water, although frequently occurring in the upper layers. *T. lucida* seems to be most common in the warmer waters of the western Pacific and in the eastern Indian Ocean; small numbers extend into the south-western Indian Ocean but the species is probably absent from the north-western part (Arabian Sea, Red Sea and Persian Gulf). *T. obscura* is most common in the northern part of the Indian Ocean, particularly the Arabian Sea; small numbers extend at least as far as 30° S in the western half of the Indian Ocean but it has not been recorded south of 10° S in the eastern half; it is probably confined to the Indian Ocean region.

Taxonomic affinities

There has been considerable disagreement among taxonomists as to the systematic position of the genus *Thalassocaris*. Dana (1852, 1854) placed his genus *Regulus* (= *Thalassocaris* Stimpson, 1860) in the Oplophorinae, which he regarded as a subfamily of the Palaemonidae. Stimpson (1860) and Kingsley (1880) adopted a similar grouping for

Thalassocaris. The genus was placed in a separate family (Thalassocaridae) by Bate (1888), who regarded it as intermediate between the Pandalidae and the Palaemonidae. The family Thalassocaridae was also recognized by Ortmann (1890), who placed it between the Alpheidae and the Pandalidae, but in 1896 he reduced it to a subfamily of the Pandalidae. De Man (1920) and Calman (1939) regarded the genus as constituting a separate family. Borradaile (1916, 1917) regarded it as a subfamily of the Pandalidae, but also included in *Thalassocaris* species which others have placed in *Chlorotocus* or *Chlorotocoides*. Kemp (1925) stressed the resemblance between *Thalassocaris* and *Chlorotocoides*, and proposed "that the subfamily Thalassocarinae should be abandoned and the genus (i.e. *Thalassocaris*) included without distinction in the Pandalidae." More recent authors have continued to disagree over the position of the genus, their attitudes being typified on the one hand by Holthuis (1955) and Thompson (1967), who recognized the monogeneric family Thalassocarididae in the superfamily Pandaloida, and on the other by Balss (1957) who followed Kemp (1925) in placing *Thalassocaris* in the Pandalidae.

Larval evidence on the taxonomic affinities of *Thalassocaris* is now available for the first time, and clearly favours the separation of the genus from the Pandalidae. The following larval characters of *Thalassocaris* contrast with those of *Pandalus* Leach and related genera: the cephalothorax is extremely broad and shallow; the rostrum remains short and without teeth until the very late zoeal stages; the antennules are relatively short, only slightly curved and not widely separated; the maxillule shows no trace of an exopod; the coxal endites of the maxilla are fused. The form of the maxillule and maxilla are of particular interest. An outer seta, representing the exopod, is present in zoeal stages I–III of all known species of *Pandalus* in which there is no marked abbreviation of larval development, and also in the early larvae of known species of *Plesionika* Bate, *Pandalina* Calman and *Dichelopandalus* Caullery; it is, however, absent from larvae of the Oplophoridae and Campylonotidae, although in other respects these show many primitive characters. *Thalassocaris* shows complete fusion of the coxal endites of the larval maxilla without any apparent reduction in the size or setation of any of the endites. This condition contrasts not only with that in larvae of the Pandalidae and Hippolytidae, in which the two coxal and two basial endites are all well developed, but also with that in larvae of the Palaemonidae and Alpheidae, in which there is only one coxal lobe but all the endites tend to be be reduced. Some approach to the condition of the larval maxilla in *Thalassocaris* is seen in *Acanthephyra* A. Milne Edwards (Oplophoridae) and *Campylonotus* Bate (Campylonotidae) in which there is partial fusion of the coxal endites with little or no reduction. Larvae of *Amphionides* Zimmer (= *Amphion* H. Milne Edwards) show some resemblance to those of *Thalassocaris* in the form of the endites of the maxilla and also in having a very broad shallow cephalothorax, but they show so many unusual features in the form of the telson, antenna, endopod of the maxilla, legs and alimentary canal that the genus cannot be regarded as closely related to *Thalassocaris* or to any other known caridean. We interpret the larval evidence as supporting the removal of *Thalassocaris* from the Pandalidae and indicating its evolution from a stem close to the Oplophoridae and Campylonotidae.

Larvae of *Chlorotocoides* are unknown, but we agree with Kemp (1925) that adult characters point to a close relationship between this genus and *Thalassocaris*. Kemp sought to show this relationship by including both genera in the Pandalidae, but we advocate the inclusion of both in the Thalassocarididae. Comparison of specimens of *C. spinicauda* and

of all three species of *Thalassocaris* confirms Kemp's (1925) observation of the presence of two pairs of organs, assumed to be photophores, of very similar position and appearance in the two genera. The pandalid *Parapandalus richardi* (Coutière) also has two pairs of photophores in the cephalothorax, and these were shown by Dennell (1940) to be formed from modified liver tubules. Dennell assumed the photophores of *Thalassocaris* and *Chlorotocoides* to be similar to those of *P. richardi* in position and derivation, but comparison of cleared specimens shows important differences in position and general appearance. In *Thalassocaris* and *Chlorotocoides* the organs in question are well defined capsules just below the cuticle, one at the base of the maxilla and one on the posterior side of the base of the fifth leg on each side; no connection with the liver could be traced from either of the organs in any of the species. In *Parapandalus* the photophores are less clearly delimited; the anterior one is at the base of the mandible and the other is deeply seated in the dorsolateral thorax, near the junction with the abdomen (i.e. much more dorsal than in the other genera). As shown by Dennell (1940). extensions of the liver enter each photophore. The photophores of *Thalassocaris* and *Chlorotocoides* therefore seem to resemble those of *Parapandalus* in assumed function only and cannot be taken as evidence of close phylogenetic relationship. It may be of significance that one of the more prominent photophores of *Oplophorus* H. Milne Edwards and *Systellaspis* Bate (Oplophoridae) is behind the base of the fifth leg, as in *Thalassocaris* and *Chlorotocoides*. This photophore is elongated in the oplophorid genera and many other photophores occur on other parts of the body (Dennell, 1940), but the similar position and lack of connection with the liver are common features which tend to support the suggestion of affinities between the Oplophoridae and the Thalassocarididae. Other adult characters common to *Oplophorus* and *Thalassocaris* are lateral expansions at the base of the rostrum, one or more median spines on the abdomen and outer teeth on the antennal scale.

Chlorotocoides has usually been considered to be closely related to *Chlorotocus*, but the rounded abdominal pleura and the lack of photophores in the latter genus are important differences. The first zoeal stage of *Chlorotocus crassicornis* (Costa) was described by Heegaard (1969); compared with the corresponding stage in *Thalassocaris*, it shows many differences, of which the presence of a long rostrum, carapace denticles, knobs on the first abdominal somite and four endites on the maxilla may be particularly mentioned. We advocate the retention of *Chlorotocus* in the Pandalidae, and the inclusion of *Chlorotocoides* with *Thalassocaris* in the Thalassocarididae.

The probable derivation of the Thalassocarididae from a stem close to the Oplophoridae may be shown by including both families in the Oplophoroidea. It must be emphasized, however, that, both as adults and larvae, the Thalassocarididae have lost several primitive characters shown by the Oplophoridae.

We are greatly indebted to Dr C. B. Goodhart, Museum of Zoology, Cambridge, England, for the loan of type material of *Thalassocaris affinis* Borradaile and *T. maldivensis* Borradaile and of other material identified by Borradaile as *T. affinis* and *T. crinitus* (*sic*); to Dr A. L. Rice, British Museum (Natural History), London, England, for opportunities to examine type material of *T. danae* Bate, *T. stimpsoni* Bate and *T. novaezealandiae* Borradaile and a specimen identified by Gurney as *T. danae*; to Dr Fenner A. Chace, Smithsonian Institution, Washington, D.C., U.S.A., for information on the type material of *T. lucida* Dana and *T. crinita* Dana; and to Dr M. J. George, Indian Ocean Biological Centre, Cochin, India, for re-examining specimens of *Thalassocaris* from tuna stomachs from the Arabian Sea.

REFERENCES

Balss, H. (1914). Ostasiatische Decapoden. II. Die Natantia und Reptantia. *Abh. bayer. Akad. Wiss.* (math.-phys. Kl.) Suppl. **2** (10): 1–101.

Balss, H. (1957). Decapoda. VIII. Systematik. *Bronn's Kl. Ordn. Tierreichs*, 5 Bd., 1 Abt., 7 Buch: 1505–1672.

Bate, C. S. (1888). Report on the Crustacea Macrura collected by H.M.S. *Challenger* during the years 1873–76. *Rep. Voy. Challenger*, Zool. **24:** xc+1–942.

Borradaile, L. A. (1915). Notes on Carides. *Ann. Mag. nat. Hist.* (8) **15:** 202–213.

Borradaile, L. A. (1916). Crustacea. Part I.—Decapoda. *Nat. Hist. Rep. Br. antarct. Terra Nova Exped.* **3**(2): 75–110.

Borradaile, L. A. (1917). On Carides from the western Indian Ocean. The Percy Sladen Trust Expedition to the Indian Ocean in 1905, under the leadership of Mr. J. Stanley Gardiner. *Trans. Linn. Soc. Lond.* (Zool.) (2) **17:** 397–412.

Calman, W. T. (1909). On Decapod Crustacea from Christmas Island, collected by Dr. W. C. Andrews. *Proc. zool. Soc. Lond.* **1909:** 703–713.

Calman, W. T. (1939). Crustacea: Caridae. *Scient. Rep. John Murray Exped.* **6:** 183–224.

Dana, J. D. (1852). Crustacea. In *United States Exploring Expedition during the years 1838–1842 under the command of Charles Wilkes, U.S.N.* **13:** xiii+1–1618.

Dana, J. D. (1854). Conspectus Crustaceorum, etc. Conspectus of the Crustacea of the Exploring Expedition under Capt. C. Wilkes, U.S.N. Macroura. *Proc. Acad. nat. Sci. Philad.* **6:** 10–28.

Dennell, R. (1940). On the structure of the photophores of some decapod Crustacea. *Discovery Rep.* **20:** 307–382.

George, M. J. & George, K. C. (1964). On the occurrence of the caridean prawn *Thalassocaris lucida* (Dana) in the stomach of *Neothunnus macropterus* (Temminck and Schlegel) from the Arabian Sea. *J. mar. biol. Ass. India* **6:** 171–172.

Gurney, R. (1942). *Larvae of Decapod Crustacea*. London: Roy. Society.

Gurney, R. & Lebour, M. V. (1941). On the larvae of certain Crustacea Macrura, mainly from Bermuda. *J. Linn. Soc. Lond.* (Zool.) **41:** 89–181.

Heegaard, P. (1969). The first larval stage of *Chlorotocus crassicornis* (Decapoda, Pandalidae). *Crustaceana* **17:** 151–158.

Holthuis, L. B. (1955). The recent genera of caridean and stenopodidean shrimps (class Crustacea, order Decapoda, supersection Natantia) with keys for their determination. *Zool. Verh.* **26:** 1–157.

Kemp, S. W. (1925). Notes on Crustacea Decapoda in the Indian Museum. XVII. On various Caridea. *Rec. Indian Mus.* **27:** 249–343.

Kingsley, J. S. (1880). On a collection of Crustacea from Virginia, North Carolina, and Florida, with a revision of the genera of Crangonidae and Palaemonidae. *Proc. Acad. nat. Sci. Philad.* **1879:** 383–427.

Man, J. G. de (1920). The Decapoda of the Siboga Expedition. Part IV. Families Pasiphaeidae, Stylodactylidae, Hoplophoridae, Nematocarcinidae, Thalassocaridae, Pandalidae, Psalidopodidae, Gnathophyllidae, Processidae, Glyphocrangonidae and Crangonidae. *Siboga Exped.* **39a3:** iv+1–328.

Ortmann, A. (E.) (1890). Die Decapodenkrebse des Strassburger Museums. I. Die Unterordnung Natantia Boas. *Zool. Jb.* (Syst.) **5:** 437–542.

Ortmann, A. E. (1896). Das System der Decapoden-Krebse. *Zool. Jb.* (Syst.) **9:** 409–453.

Stimpson, W. (1860). Prodromus descriptionis animalium evertebratorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem, a Republica Federata missa, Cadwaladaro Ringgold et Johanne Rodgers Ducibus, observavit et descripsit. Pars VIII. Crustacea Macrura. *Proc. Acad. nat. Sci. Philad.* **1860:** 22–47.

Thompson, J. R. (1967). Comments on phylogeny of section Caridea (Decapoda Natantia) and the phylogenetic importance of the Oplophoroidea. *Proc. Symp. Crustacea mar. biol. Ass. India* **1:** 314–326.

Williamson, D. I. (1969). Names of larvae in the Decapoda and Euphausiacea. *Crustaceana* **16:** 210–213.

Williamson, D. I. (1970). On a collection of planktonic Decapoda and Stomatopoda (Crustacea) from the east coast of the Sinai Peninsula, Northern Red Sea. *Bull. Sea Fish. Res. Stn Haifa* **56:** 1–48.

Zarenkov, N. A. (1968). Novye dannye o redkikh krevetkakh (Thalassocaridae, Rhynchocinetidae, Stylodactylidae, Campylonotidae, Psalidopodidae). *Byull. Mosk. Obshch. Ispyt. Prir.* (Biol.) **73** (3): 57–62.