Plankton Benthos Res 1(1): 26–41, 2006

Plankton & Benthos Research

Descriptions of phyllosoma larvae of *Scyllarus bicuspidatus* and *S. cultrifer* (Decapoda, Scyllaridae) collected in Japanese waters

Nariaki Inoue & Hideo Sekiguchi*

Faculty of Bioresource, Mie University, 1515 Kamihama-cho, Tsu, Mie 514–8507, Japan

Received 7 September 2004; Accepted 5 August 2005

Abstract: For understanding larval recruitment processes of *Scyllarus* and *Panulirus* lobsters, exact species identification of field-caught phyllosoma larvae, particularly those of the early stages, is essential. Using ichthyoplankton samples from waters along the west coast of Kyushu to the Japan Sea coast of Honshu and the Kuroshio and Kuroshio-Counter Current regions, we described morphological features of the I to VIII (final) stage phyllosoma larvae of S. bicuspidatus and the IV to VIII stage larvae of *S. cultrifer*. The larvae of equivalent stages of two *Scyllarus species* are distinguishable from each other by using the combinations of body lengths and morphological features of antennules, pereiopods and pleopods. In addition, a) equivalent larval stages in *S. cultifer* are always larger than in *S. bicuspidatus*; b) cephalic shield of *S. bicuspidatus* is rounder than in *S. cultrifer*; c) relative to antennule length, the eyestalk is longer in *S. cultrifer* than in *S. bicuspidatus*.

Key words: Phyllosoma larvae, Identification, Japanese waters, *Scyllarus bicuspidatus*, *Scyllarus cultrifer*

Introduction

Scyllarid and palinurid lobsters are classified into three families (Palinuridae, Scyllaridae and Synaxidae) and share a long planktonic life period as phyllosoma larvae. Of these lobsters, the adult of *Scyllarus* and *Panulirus* species can be common and abundant in the coastal waters of Japan as well as in other temperate and tropical waters, including New Zealand and Australian waters. Most of the large-sized *Panulirus* species are commercially important and are targets for fisheries, whereas small-sized *Scyllarus* species, despite having the largest species number among the scyllarid and palinurid lobsters, are of a low commercial value. In contrast to the *Panulirus* species, *Scyllarus* species are usually dominant among the phyllosoma larvae collected in coastal waters (Inoue et al. 2000, 2001, 2004).

There are many studies about larval recruitment processes of palinurid species, including larval distribution and larval transport/dispersal of *Panulirus* (Booth & Phillips 1994, Sekiguchi & Inoue 2002). However, few studies about scyllarid species exist (e.g. Inoue et al. 2000, 2001, 2004, Booth et al. 2005). According to the larval recruitment studies of *Panulirus*, phyllosoma larvae flush out from coastal waters into oceanic waters, and once again return to the coastal waters where they metamorphose into the puerulus stage to settle (Booth & Phillips 1994, Sekiguchi & Inoue 2002). Of course, for understanding the population dynamics of *Scyllarus*, we need to have enough information on the mechanisms of larval retention or larval transport/dispersal from coastal waters into oceanic waters and the reverse. Further, larval recruitment studies of *Scyllarus* contribute to additional resolution of unresolved recruitment processes in *Panulirus*. Accordingly, exact identification to the species level of field-caught phyllosoma larvae, particularly in the early stages, is essential for understanding larval recruitment processes of *Scyllarus* lobsters, as well as *Panulirus* ones.

A total of 11 adult *Scyllarus* species have been reported to date in Japan and its neighbouring waters (Sekiguchi & Inoue 2002): *S. aurora*, *S. bicuspidatus*, *S. batei*, *S. bertholdii*, *S. brevicornis*, *S. cultrifer*, *S. formosanus*, *S. kitanoviriosus*, *S. longidactilus*, *S. martensii*, and *S. rugosus*. *Scyllarus* species, particularly three species (*S. bicuspidatus*, *S. cultrifer* and *S. kitanoviriosus*) are known to be abundant and dominant among the phyllosoma larvae collected in the same waters (Wada et al. 1985, Sekiguchi 1986a, b, Inoue et al. 2000, 2001, 2004, Higa & Shokita

* Corresponding author: Hideo Sekiguchi; E-mail, sekiguch@bio.mie-u.ac.jp

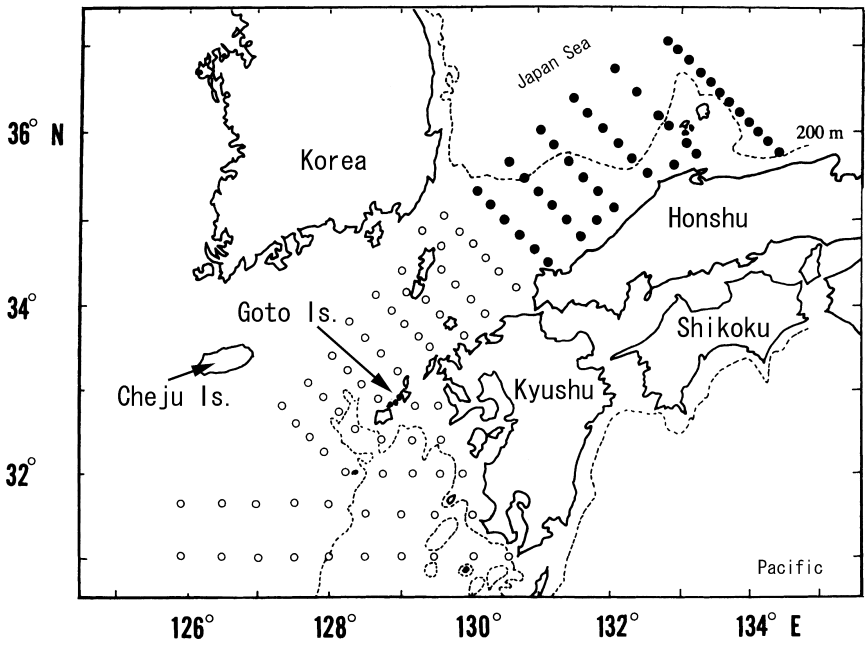

Fig. 1. Map of the study area and location of sampling stations in waters along the west coast of Kyushu to the Japan Sea coast of Honshu. Open and solid circles: stations with sampling by 80 RN net and both 80 RN and 130 N nets, respectively; dotted lines, isopleths of 200 m depth (From Inoue et al. 2000).

2004). Of all the *Scyllarus* phyllosoma larvae in the world, the morphological features of the first to final stage phyllosoma larvae have been examined only for *S. americanus*, *S. martensii* and *S. demani* (Robertson 1968, Phillips & McWilliam 1986, Ito & Lucas 1990).

We examine and describe here morphological features of the first to final (VIII) stage phyllosoma larvae of *S. bicuspidatus* and the IV to VIII stage larvae of *S. cultrifer*, based on phyllosoma specimens collected in Japanese waters.

Materials and Methods

Specimens examined in the present study came from two sources: 1) 140 ichthyoplankton samples from waters along the west coast of Kyushu to the Japan Sea coast of Honshu from Oct.13 to Nov.20, 1984 (Fig. 1), and 2) 286 samples from the Kuroshio and Kuroshio-Counter Current regions from Mar.16 to July 22 in 1984–1986 (Fig. 2). Details of samples and sampling methods are given in Inoue et al. (2000, 2001, 2004). Based on phyllosoma larvae included in the above ichthyoplankton samples, distribution patterns and species and stage compositions of phyllosoma larvae have already been examined in Inoue et al. (2000, 2004) and Inoue & Sekiguchi (2001).

Samples were fixed in 10% formalin seawater immediately after sampling. Phyllosoma larvae of the genus *Scyllarus* were sorted out from the samples in the laboratory. Body length (BL), cephalon length (CL), cephalon width (CW) and thorax width (TW) were measured. Late stage (VII and VIII) phyllosoma larvae were identified to the species level according to Sekiguchi & Inoue (2002) and Inoue et al. (2004). Then, early to middle (I to VI) stage phyllosoma larvae of *Scyllarus* species were identified to species based on similarities of morphological features to later stage ones already identified according to Sekiguchi & Inoue (2002) and Inoue et al. (2004). Specimens of stages I to VIII phyllosoma larvae of *S. bicuspidatus* and stages IV to VIII of *S. cultrifer* were thereby obtained.

Developmental aspects and nomenclature of these phyllosoma larvae were described following Phillips & McWilliam (1986). In all phyllosoma larvae, the maxillipeds and where fully developed, the pereiopods, consist of five segments. From proximal to distal, these are: 1) coxa, 2) basis (both=the protopod) from which the endopod and exopod later arise. The joint of the basis with the ischium of the endopod is never apparent, and the ischium and merus are fused so that in the larvae we only see a fused basis+ischiomerus as a second segment, 3) carpus, 4) propodus and 5) dactylus. All phyllosoma specimens were observed, and different stage phyllosoma larvae of the same species have very similar morphological features. Accordingly, we described morphological features based on one specimen each.

Holthuis (2002) revised the Indo-Pacific adult species of the genus *Scyllarus* and divided the traditional genus *Scyllarus* into 14 genera (*Acantharctus*, *Antarctus*, *Antipodarctus*, *Bathyarctus*, *Biarctus*, *Chelarctus*, *Crenarctus*, *Eduarctus*, *Galearctus*, *Gibbularctus*, *Petrarctus*, *Remiarctus*, *Scammarctus*, and *Scyllarus*). However, to avoid confusion, we used the traditional genus name *Scyllarus* in the text of this paper and then the new genus and species names together with the traditional ones in our tables and figures,

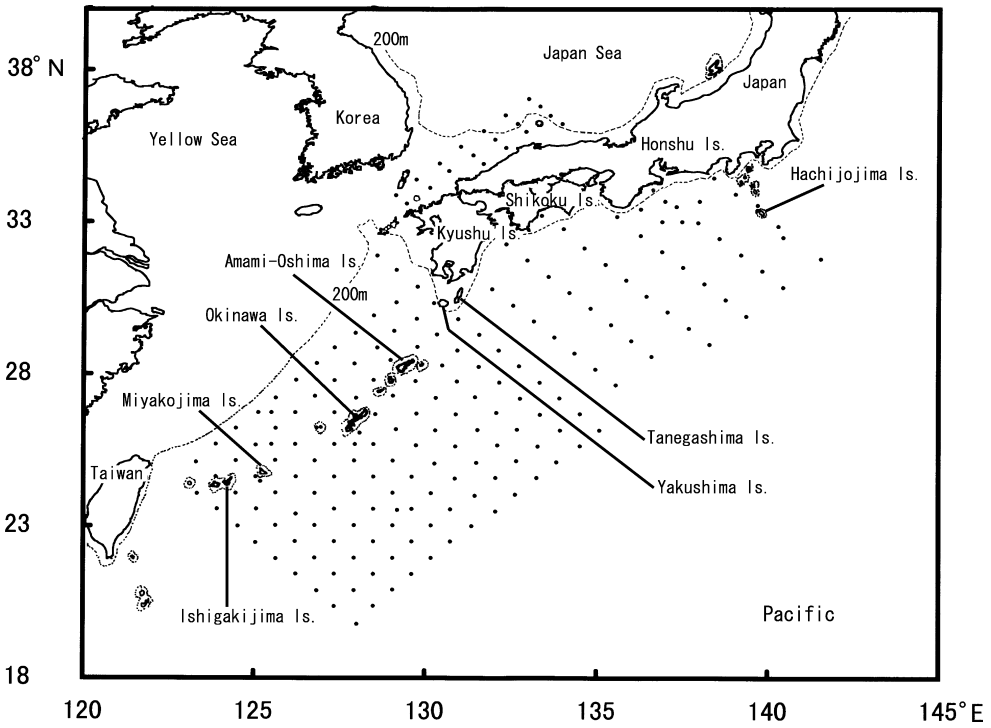

Fig. 2. Map of the study area and location of sampling stations in the Kuroshio and Kuroshio Counter-Current regions. Dots, sampling stations in the present study; dotted lines, isopleths of 200m depth (From Inoue & Sekiguchi 2005).

because Holthuis' (2002) revision includes drastic changes in the traditional taxonomy of the previous genus *Scyllarus* and we believe this has not yet been incorporated by other lobster taxonomists (see Inoue et al. 2004).

Morphological Descriptions

a) *Scyllarus bicuspidatus*

Stage I (Fig. 3)

BL, 1.1–1.2 mm (mean 1.2 mm, n=3). CL, CW and TW could not be measured due to damage in two specimens. We described morphological features of a larva (BL 1.2 mm) collected at 33°17.6′N, 128°56.1′E on Oct. 31, 1986; CL, 0.7 mm; CW, 0.8 mm; TW, 0.5 mm; CL/CW, 0.9 mm and CW/TW, 1.6 mm.

Cephalon (Fig. 3A) wider than long, nearly twice width of thorax, covering the bases of 3rd maxilliped. Eye and stalk (Fig. 3B) nearly same length as antennule, eye stalk unsegmented. Antennule (Fig. 3B) uniramous and unsegmented, bearing 1 relatively long subterminal seta and at least 4 minute terminal setae; antenna (Fig. 3B) much shorter than antennule, uniramous and unsegmented, bearing at least 2 minute subterminal setae. First maxilla (Fig. 3D) biramous and unsegmented, anterior lobe with 2 stout masticatory spines plus 3 short setae, posterior lobe with 1 long and 2 short terminal setae; 2nd maxilla (Fig. 3C) uniramous and 2 segemented, bearing 4 long terminal setae. Second and 3rd maxillipeds (Figs. 3A, C) uniramous and 5 segmented; 2nd maxilliped with distal end of dactylus sharply projecting, bearing 1 seta on 2nd and 3rd segment, at least 6 setae on propodus and 4 setae on dactylus; 3rd maxilliped bearing 1 ventral coxal spine and at least 4 setae on propodus and dactylus. Pereiopods (Fig. 3A) lacking 4th and 5th ones, 1st to 3rd pereiopods bearing 1 ventral coxal and subexopodal spines, and also distal end of dactylus sharply projecting; 1st and 2nd pereiopods biramous and 5 segmented with exopod bearing 5 pairs of natatory setae; 3rd pereiopod uniramus and 5 segmented, bearing exopod bud. Abdomen (Figs. 3E, F) slightly longer than 1/3 of hindbody length, tapering much posteriorly, lacking pleopods and uropods. Telson (Figs. 3E, F) undifferentiated from abdomen.

Stage II (Fig. 4)

BL (n=11), 1.4–1.7 mm (mean 1.6 mm); CL, 0.8–1.0 mm (mean 0.9 mm); CW, 0.9–1.2 mm (mean 1.1 mm); TW, 0.5–0.6 mm (mean 0.6 mm); CL/CW, 0.8–0.9 (mean 0.9); CW/TW, 1.6–2.4 (mean 1.9). Of these larval specimens, we described the morphological features of a larva (BL 1.6 mm) collected at 33°51.9′ N, 128°16.2′E on Oct. 31, 1986.

Eye and stalk (Fig. 4B) slightly longer than antennule, eye stalk segmented. Antennule (Fig. 4B) bearing at least 6 minute terminal setae and bud-like projection with 1 short seta. Second maxilla (Fig. 4C) with 2 short setae on 1st segment. Third maxilliped (Fig. 4A) with at least 5 setae on propodus. Pereiopods (Fig. 4A) lacking 5th one, bearing

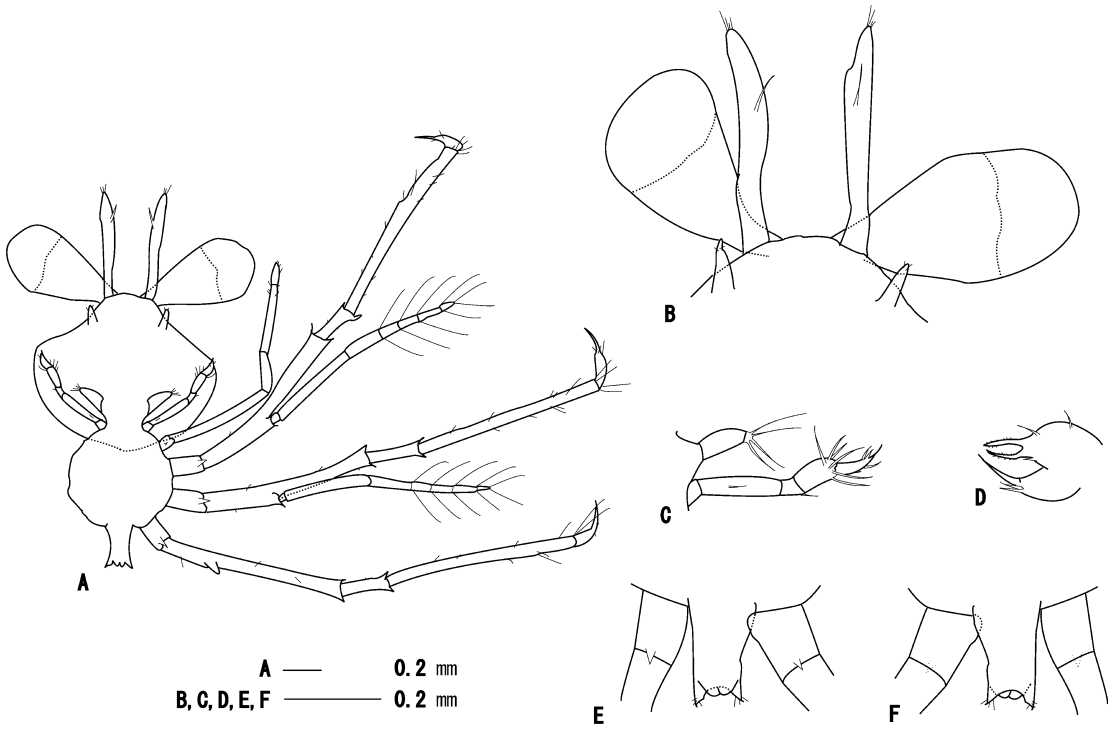

Fig. 3. Phyllosoma larva of *Scyllarus bicuspidatus* (*Crenarctus bicuspidatus*), stage I. A, ventral view; B, ventral view of eye, antennule and antenna; C, 2nd maxilla and 2nd maxilliped; D, 1st maxilla; E, ventral view of 3rd pereiopod and abdomen; F, dorsal view of 3rd pereiopod and abdomen. Parenthetic names are new genera and species names established by Holthuis (2002).

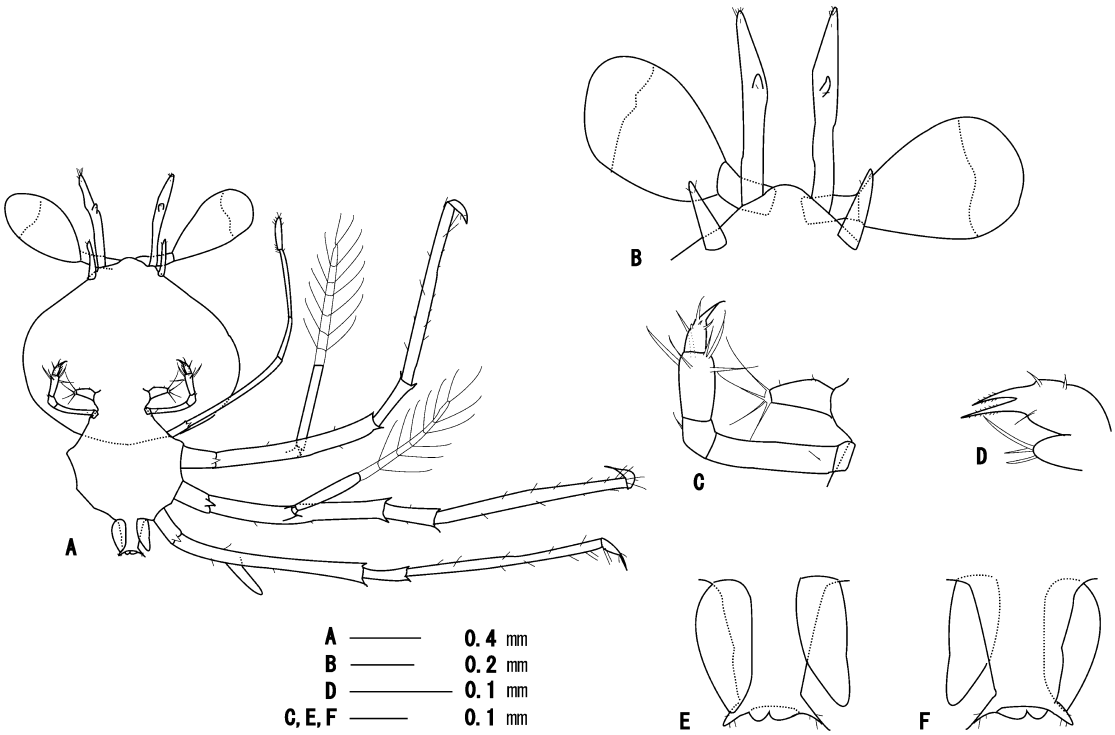

Fig. 4. Phyllosoma larva of *Scyllarus bicuspidatus* (*Crenarctus bicuspidatus*), stage II. A, ventral view; B, ventral view of eye, antennule and antenna; C, 2nd maxilla and 2nd maxilliped; D, 1st maxilla; E, ventral view of 4th pereiopod and abdomen; F, dorsal view of 4th pereiopod and abdomen. Parenthetic names are new genera and species names established by Holthuis (2002).

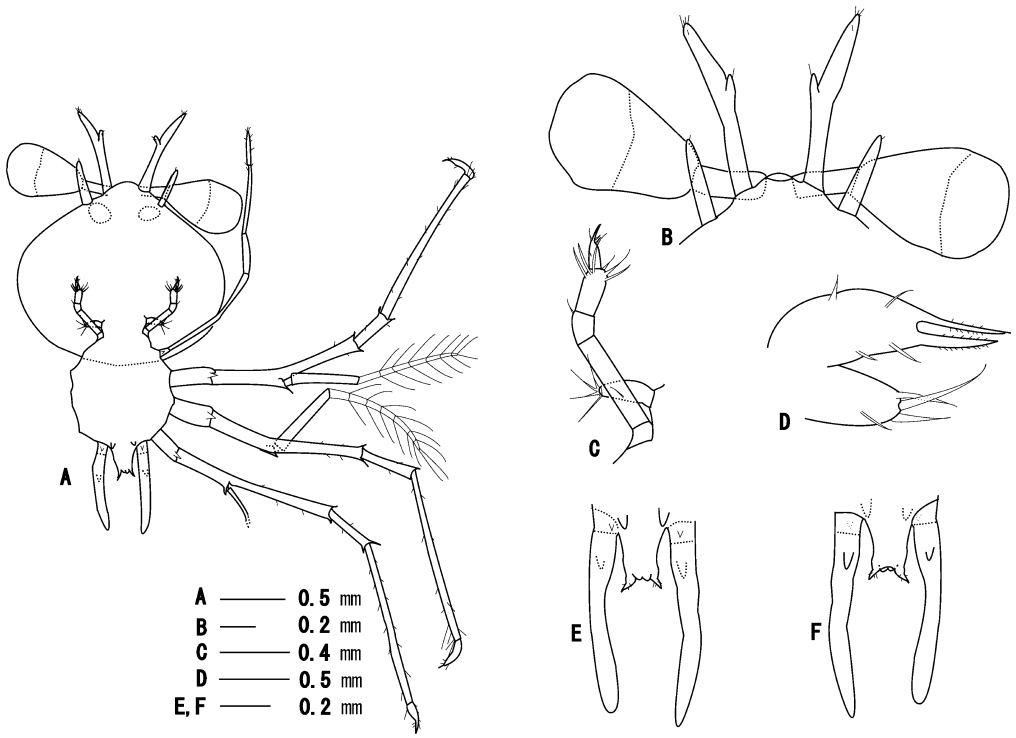

Fig. 5. Phyllosoma larva of *Scyllarus bicuspidatus* (*Crenarctus bicuspidatus*), stage III. A, ventral view; B, ventral view of eye, antenule and antenna; C, 2nd maxilla and 2nd maxilliped; D, 1st maxilla; E, ventral view of 4th and 5th pereiopods and abdomen; F, dorsal view of 4th and 5th pereiopods and abdomen. Parenthetic names are new genera and species names established by Holthuis (2002).

ventral coxal spine except for 4th pereiopod; exopods of 1st and 2nd pereiopods bearing 7 and 6 pairs of natatory setae, respectively; 3rd pereiopod with bud-like exopod lacking any seta; 4th pereiopod elongate bud as long as abdomen. Telson (Figs. 4E, F) with strong postero-lateral angles. Other characters as in stage I.

Stage III (Fig. 5)

BL (n=15), 2.1–2.4 mm (mean 2.2 mm); CL, 1.3–1.5 mm (mean 1.4 mm); CW, 1.5–1.8 mm (mean 1.6 mm); TW, 0.7–1.0 mm (mean 0.8 mm); CL/CW, 0.8–1.0 (mean 0.9); CW/TW, 1.8–2.4 (mean 2.1). Of these larval specimens, we described the morphological features of a larva (BL 2.2 mm) collected at 33°06.3′N, 128°29.8′E on Nov. 1, 1986.

Antennule (Fig. 5B) bearing at least 5 minute terminal setae; antenna (Fig. 5B) with at least 1 minute terminal seta. First maxilla (Fig. 5D) with anterior lobe bearing 2 stout masticatory terminal spines plus 4 short setae and with posterior lobe bearing 1 long and 2 short terminal setae plus 1 short subterminal seta. Third maxilliped (Fig. 5A) propodus and dactylus bearing at least 3 and 7 setae, respectively. Pereiopods (Fig. 5A), except for 4th and 5th ones bearing ventral coxal and subexopodal spines; exopods of 1st and 2nd pereiopods bearing 7 pairs of natatorial setae; 3rd pereiopod with damaged exopod; 4th pereiopod with bud-like projection, extending for beyond telson; 5th pereiopod (Figs. 5E, F) bud. Other characters as in stage II.

Stage IV (Fig. 6)

BL (n=23), 2.8–3.5 mm (mean 3.2 mm); CL, 1.7–2.3 mm (mean 2.1 mm); CW, 2.0–2.6 mm (mean 2.3 mm); TW, 1.0–1.3 mm (mean 1.1 mm); CL/CW, 0.8–1.0 (mean 0.9); CW/TW, 1.9–2.3 (mean 2.0). Of these larval specimens, we described the morphological features of a larva (BL 3.2 mm) collected at 31°29.8′N, 129°59.6′E on Nov. 5, 1986.

Cephalon (Fig. 6A) with low, stout spine near each antennule base on dorsal surface of cephalon. Eye and stalk (Fig. 6B) extending for beyond antennule. Antennule (Fig. 6B) bearing at least 10 minute setae along inner margin and projection; antenna (Fig. 6B) bearing lateral process and at least 1 minute subterminal seta. First maxilla (Fig. 6D) with 4 short terminal setae plus 1 short seta on posterior lobe. Third maxilliped (Fig. 6A) propodus and dactylus bearing at least 6 and 9 setae, respectively. Pereiopods (Fig. 6A) bearing ventral coxal and subexopodal spines except for 4th and 5th ones; exopods of 1st to 3rd pereiopods bearing 9, 9 and 7 pairs of natatory setae, respectively; 4th pereiopod 5 segmented with exopod bud; 5th pereiopod bud. Abdomen (Figs. 6E, F) bearing uropod bud lacking pleopods; telson (Figs. 6E, F) beginning to differentiate from abdomen. Other characters as in stage III.

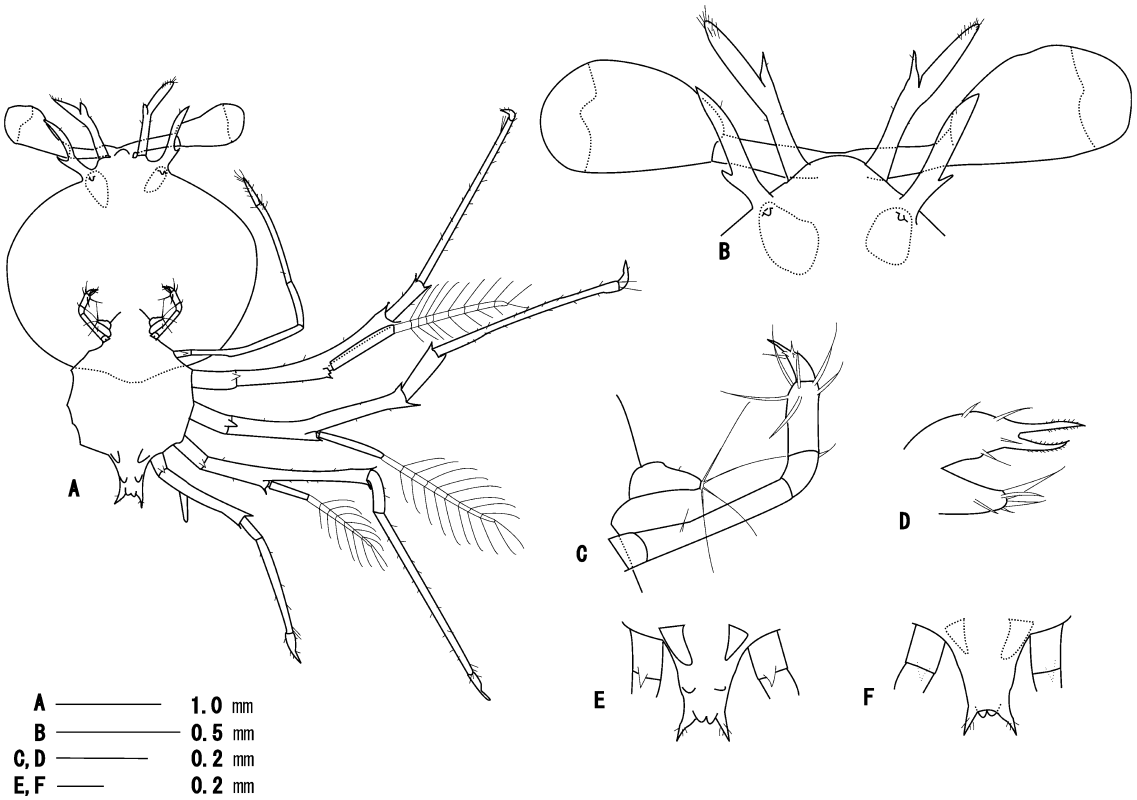

Fig. 6. Phyllosoma larva of *Scyllarus bicuspidatus* (*Crenarctus bicuspidatus*), stage IV. A, ventral view; B, ventral view of eye, antennule and antenna; C, 2nd maxilla and 2nd maxilliped; D, 1st maxilla; E, ventral view of 4th and 5th pereiopods and abdomen; F, dorsal view of 4th and 5th pereiopods and abdomen. Parenthetic names are new genera and species names established by Holthuis (2002).

Stage V (Fig. 7)

BL (n=31), 3.6–4.9 mm (mean 4.3 mm); CL, 2.3–3.4 mm (mean 3.0 mm); CW, 2.7–3.7 mm (mean 3.3 mm); TW, 1.3–1.8 mm (mean 1.6 mm); CL/CW, 0.7–1.1 (mean 0.9); CW/TW, 1.9–2.3 (mean 2.1). Of these larval specimens, we described the morphological features of a larva (BL 4.1 mm) collected at 33°06.3′N, 128°29.8′E on Nov. 1, 1986.

Antennule (Fig. 7B) biramous and 2 segmented, outer flagellum bearing at least 14 minute setae on inner margin; antenna (Fig. 7B) shorter than antennule, flattened and unsegmented, bearing at least 4 minute setae and lateral process (directed anteriorly) with pointed tip. First maxilla (Fig. 7E) with anterior lobe bearing 3 stout masticatory terminal spines plus 4 short setae and with posterior lobe bearing 2 long and 2 short terminal setae plus 1 short subterminal seta; 2nd maxilla (Fig. 7D) more lobulate. Second maxilliped (Figs. 7C, D) bearing at least 8 setae on propodus; 3rd maxilliped (Fig. 7A) with rudiment of exopod appearing as slight protrusion. Pereiopods (Fig. 7A), except for 5th one, bearing ventral coxal and subexopodal spines; exopods of 1st to 4th pereiopods bearing 10, 10, 8 and 4 pairs of natatorial setae, respectively; 5th pereiopod elongate bud lacking any setae or spines, much shorter than telson. First appearance of pleopod buds (Fig. 7F), on abdomen; uropods (Fig. 7F) oval bud. Other characters as in stage IV.

Stage VI (Fig. 8)

BL (n=37), 5.1–7.3 mm (mean 6.2 mm); CL, 3.4–4.9 mm (mean 4.1 mm); CW, 3.9–5.6 mm (mean 4.6 mm); TW, 1.8–2.5 mm (mean 2.2 mm); CL/CW, 0.9–1.0 (mean 0.9); CW/TW, 1.9–2.5 (mean 2.1). Of these larval specimens, we described the morphological features of a larva (BL 6.7 mm) collected at 33°32.1′N, 129°24.1′E on Oct. 31, 1986.

Antennule (Fig. 8B) 3 segmented, outer flagellum bearing at least 15 minute setae on inner margin; antenna (Fig. 8B) slightly longer than antennule. First maxilla (Fig. 8E) posterior lobe bearing 2 long and 3 short terminal setae plus 3 short subterminal setae; 2nd maxilla (Fig. 8D) bud-like without 4 terminal setae. First appearance of 1st maxilliped (Fig. 8D) bud; 2nd maxilliped (Fig. 8C) bearing at least seven setae on propodus. Pereiopods (Fig. 8A) bearing one ventral coxal spine; exopods of 1st and 2nd pereiopods bearing 15 and 16 pairs of natatorial setae, respectively (exopods of 3rd and 4th pereiopods damaged); 5th pereiopod (Figs. 8F, G) elongate and 2 segmented bud, bearing at least 1 short seta on 2nd segment. Pleopod buds (Fig. 8F) notched; uropods (Figs. 8F, G) biramous and oval buds, not extending beyond telson; telson shape differs from stage V

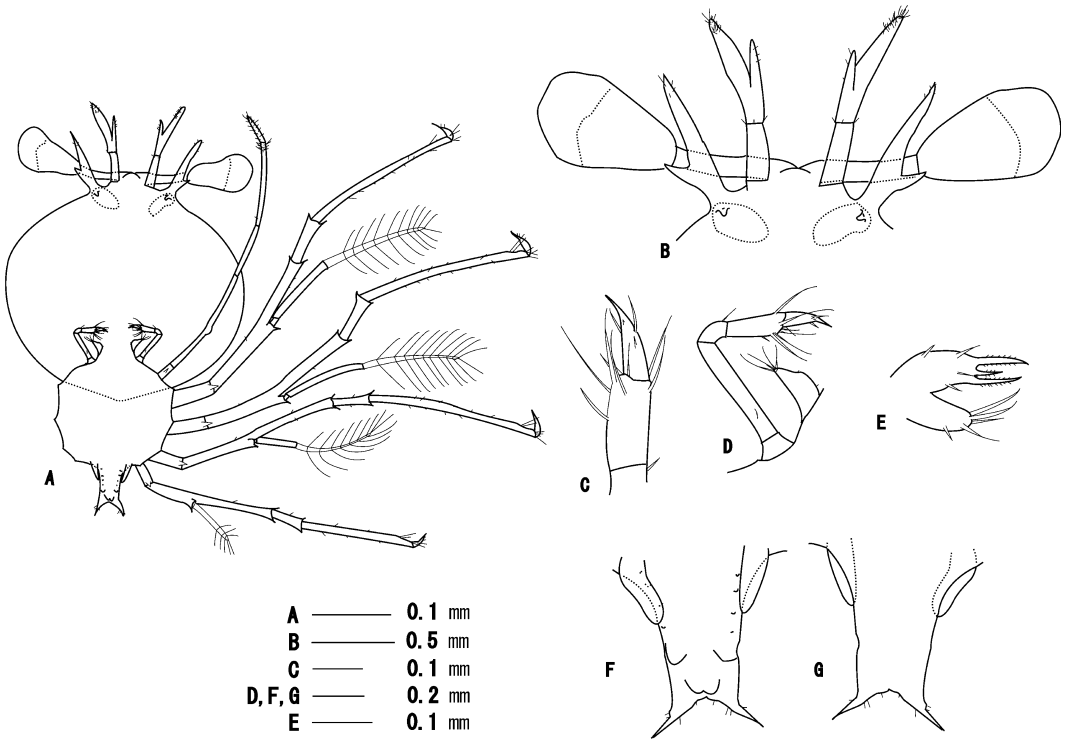

Fig. 7. Phyllosoma larva of *Scyllarus bicuspidatus* (*Crenarctus bicuspidatus*), stage V. A, ventral view; B, ventral view of eye, antennule and antenna; C, distal end of 2nd maxilliped; D, 2nd maxilla and 2nd maxilliped; E, 1st maxilla; F, ventral view of 5th pereiopod and abdomen; G, dorsal view of 5th pereiopod and abdomen. Parenthetic names are new genera and species names established by Holthuis (2002).

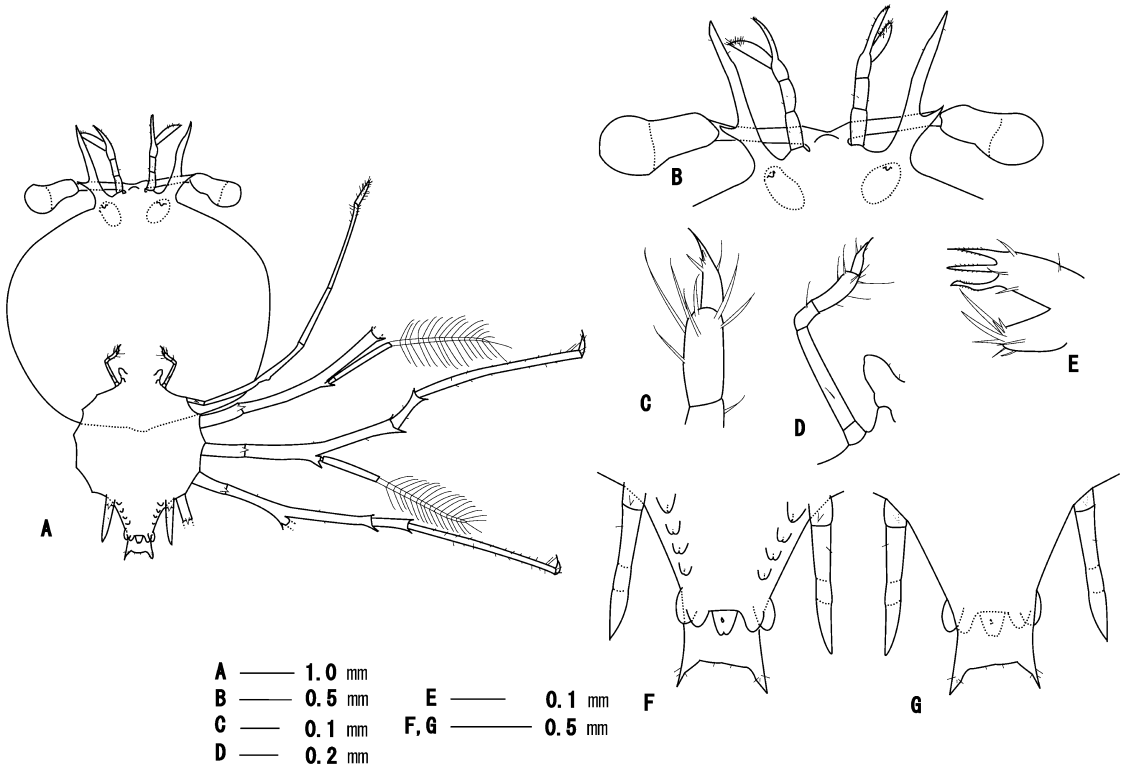

Fig. 8. Phyllosoma larva of *Scyllarus bicuspidatus* (*Crenarctus bicuspidatus*), stage VI. A, ventral view; B, ventral view of eye, antennule and antenna; C, distal end of 2nd maxilliped; D, 2nd maxilla, 1st and 2nd maxillipeds; E, 1st maxilla; F, ventral view of 5th pereiopod and abdomen; G, dorsal view of 5th pereiopod and abdomen. Parenthetic names are new genera and species names established by Holthuis (2002).

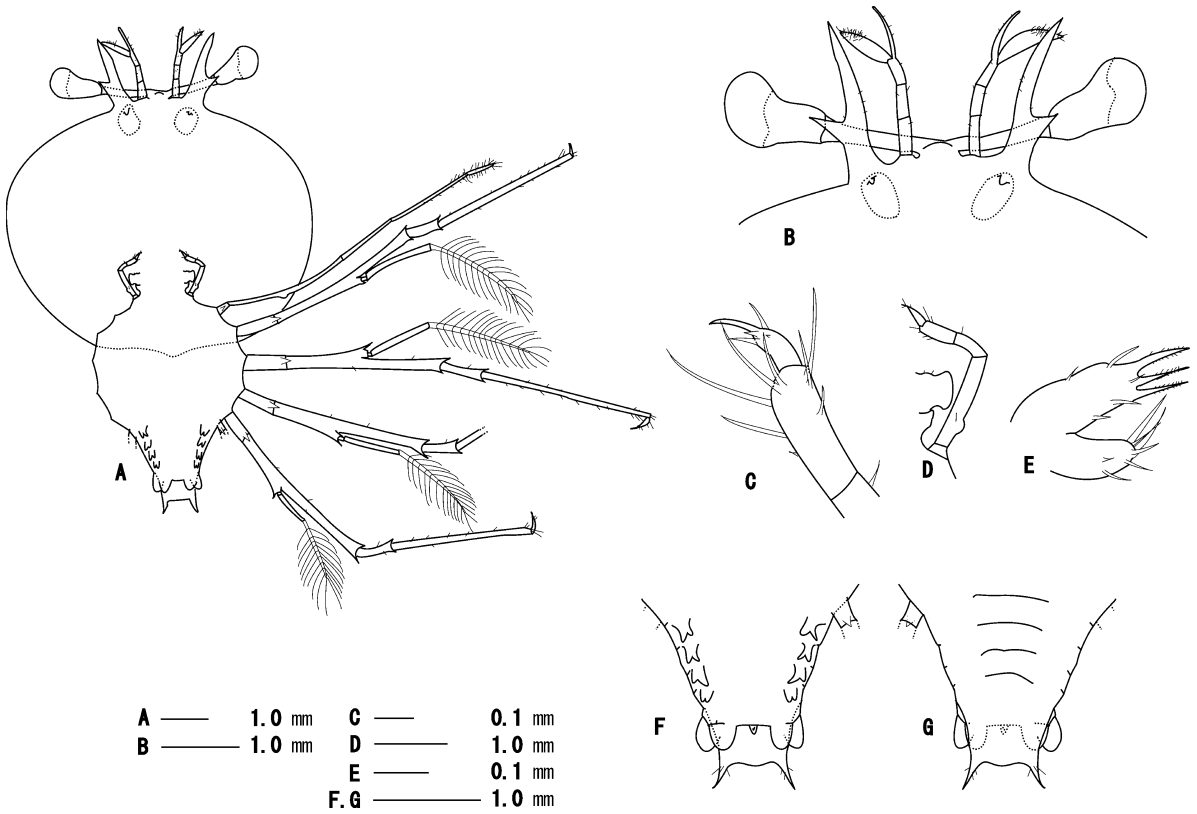

Fig. 9. Phyllosoma larva of *Scyllarus bicuspidatus* (*Crenarctus bicuspidatus*), stage VII. A, ventral view; B, ventral view of eye, antennule and antenna; C, distal end of 2nd maxilliped; D, 2nd maxilla, 1st and 2nd maxillipeds; E, 1st maxilla; F, ventral view of abdomen; G, dorsal view of abdomen. Parenthetic names are new genera and species names established by Holthuis (2002).

(cf. Figs. 7F, G and 8F, G). Other characters as in stage V.

Stage VII (Fig. 9)

BL (n=15), 8.2–10.0 mm (mean 9.2 mm); CL, 5.2–6.2 mm (mean 5.8 mm); CW, 5.9–7.2 mm (mean 6.7 mm); TW, 2.7–3.9 mm (mean 3.2 mm); CL/CW, 0.8–0.9 (mean 0.9); CW/TW, 1.9–2.2 (mean 2.1). Of these larval specimens, we described the morphological features of a larva (BL 8.2 mm) collected at 31°00.0′N, 129°29.5′E on Nov. 8, 1986.

Cephalon (Fig. 9A) leaving the bases of 1st pereiopod exposed. Antennule (Fig. 9B) outer flagellum bearing at least 20 minute setae on its inner margin. First maxilla (Fig. 9E) with anterior lobe bearing 3 stout masticatory terminal spines plus 5 short setae and with posterior lobe bearing 2 long and 2 short terminal setae plus 3 short subterminal seta; 2nd maxilla (Fig. 9D) with developed scaphognathite lacking terminal setae. First maxilliped (Fig. 9D) small bud; 2nd maxilliped (Figs. 9C, D) with rudiment of exopod appearing as a slight protrusion, bearing at least 8 setae on propodus. Exopods of 1st to 4th pereiopods (Fig. 9A) bearing 13, 15, 13 and 10 pairs of natatory setae, respectively; 5th pereiopod (Figs. 9A, F, G) difficult to observe due to damaged appendages. Abdomen (Figs. 9F, G) beginning to be segmented; 1st to 4th pleopods (Fig. 9F) bilobed; uropods (Figs. 9F, G) enlarged and biramous, not extending beyond telson. Other characters almost as in stage VI.

Stage VIII (final phyllosoma stage) (Fig. 10)

BL (n=7), 12.5–14.3 mm (mean 13.3 mm); CL, 7.3–8.0 mm (mean 7.6 mm); CW, 8.3–9.4 mm (mean 8.8 mm); TW, 4.3–4.9 mm (mean 4.5 mm); CL/CW, 0.8–0.9 (mean 0.8); CW/TW, 1.9–2.0 (mean 1.9). Of these larval specimens, we described the morphological features of a larva (BL 12.7 mm) collected at 34°27.5′N, 129°34.6′E on Oct. 27, 1986.

First maxilla (Fig. 10E) posterior lobe with 2 long and two short terminal setae plus 4 short subterminal setae; 2nd maxilla (Fig. 10D) with more developed scaphognathite. First maxilliped (Fig. 10D) bilobate, 2nd maxilliped (Figs. 10C, D) bearing at least 5 setae on dactylus. Pereiopods (Fig. 10A) bearing gill-buds on coxal segment except for 5th pereiopod; exopods of 1st to 4th pereiopods bearing 16, 16, 16 and 11 pairs of natatory setae, respectively; 5th pereiopod (Figs. 10F, G) uniramous and 4 segmented, bearing at least 9 short setae. Abdomen (Figs. 10F, G) 4 segmented, slightly longer than 1/2 of hindbody length; pleopods (Fig. 10F) biramous and unsegmented; uropods more enlarged than stage VII (cf. Figs. 9F, G and 10F, G). Other characters as in stage VII.

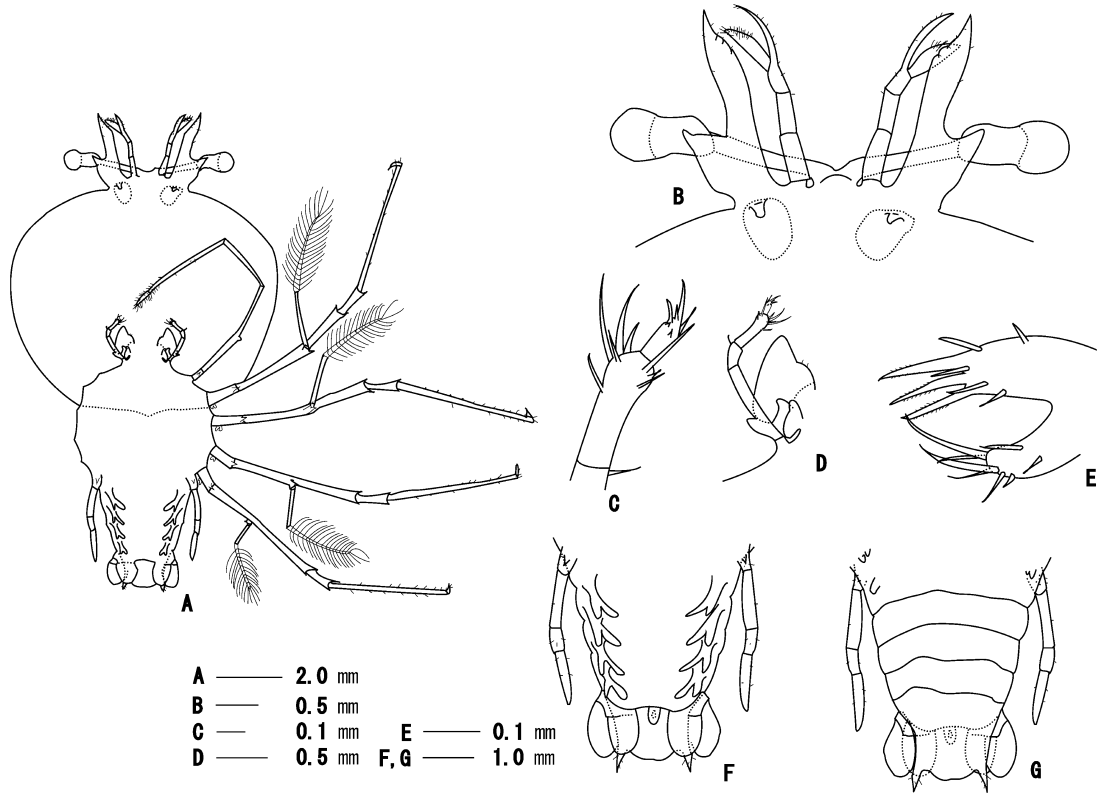

Fig. 10. Phyllosoma larva of *Scyllarus bicuspidatus* (*Crenarctus bicuspidatus*), stage VIII. A, ventral view; B, ventral view of eye, antennule and antenna; C, distal end of 2nd maxilliped; D, 2nd maxilla, 1st and 2nd maxillipeds; E, 1st maxilla; F, ventral view of 5th pereiopod and abdomen; G, dorsal view of 5th pereiopod and abdomen. Parenthetic names are new genera and species names established by Holthuis (2002).

b) *Scyllarus cultrifer*

Stage IV (Fig. 11)

BL (n=22), 5.8–8.9 mm (mean 7.8 mm); CL, 4.0–6.0 mm (mean 5.3 mm); CW, 4.4–7.2 mm (mean 6.1 mm); TW, 2.2–3.2 mm (mean 2.8 mm); CL/CW, 0.8–0.9 (mean 0.9); CW/TW, 2.0–2.5 (mean 2.2). Of these larval specimens, we described the morphological features of a larva (BL 7.5 mm) collected at 25°39.6′N, 128°31.9′E on May. 31, 1984.

Cephalon (Fig. 11A) slightly wider than long, nearly twice the width of the thorax, reaching the bases of 1st pereiopod, with low, stout spine near each antenna base on the dorsal surface. Eye and stalk (Fig. 11B) much longer than antennule, eye stalk segmented. Antennule (Fig. 11B) biramous and 3 segmented, outer flagellum bearing at least 10 minute setae on inner margin; antenna (Fig. 11B) slightly longer than antennule, flattened and unsegmented, bearing at least one minute seta and a lateral process (directed laterally) with a pointed tip. First maxilla (Fig. 11D) biramous and unsegmented, anterior lobe with 3 stout masticatory spines plus 4 short setae, posterior lobe with 2 long (1 seta damaged) and 2 short terminal setae plus 1 short subterminal seta; 2nd maxilla (Fig. 11C) bud. Second maxilliped (Fig. 11C) uniramous and 5 segmented with distal end of dactylus sharply projecting, bearing 1 seta on 2nd and 3rd segments, at least 7 setae on propodus and 4 setae on dactylus, respectively; 3rd maxilliped (Fig. 11A) uniramous and 5 segmented, bearing 1 ventral coxal spine and at least 5 setae on propodus and 19 setae on dactylus, respectively. Pereiopods (Fig. 11A), except for 5th pereiopod, bearing ventral coxal and subexopodal spines with distal end of dactylus sharply projecting; exopods of 1st to 4th pereiopods with 5 segments bearing 14, at least 8 (tip damaged), 12 and 10 pairs of natatory setae, respectively; 5th pereiopod (Figs. 11E, F) bud. Abdomen (Figs. 11E, F) unsegmented, slightly shorter than 1/4 of hindbody length, tapering posteriorly. Telson (Figs. 11E, F) begining to differentiate from abdomen, with strong postero-lateral angles.

Stage V (Fig. 12)

BL (n=6), 9.4–11.1 mm (mean 10.4 mm); CL, 6.6–7.5 mm (mean 7.1 mm); CW, 7.7–9.0 mm (mean 8.5 mm); TW, 3.7–4.0 mm (mean 3.9 mm); CL/CW, 0.8–0.9 (mean 0.8); CW/TW, 2.1–2.3 (mean 2.2). Of these larval specimens, we described the morphological features of a larva (BL 11.1 mm) collected at 30°15.0′N, 132°34′E on Aug. 5, 1984.

Antennule (Fig. 12B) outer flagellum bearing at least 19 minute setae on inner margin; antenna (Fig. 12B) with at least 5 minute setae. First maxilla (Fig. 12E) bearing 5

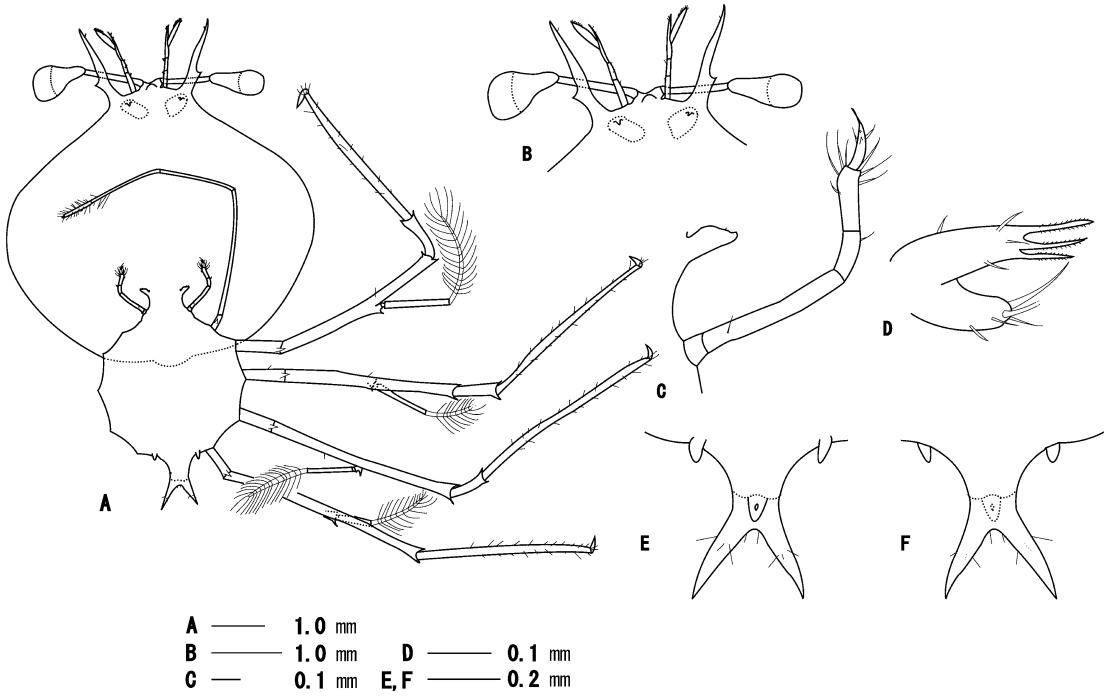

Fig. 11. Phyllosoma larva of *Scyllarus cultrifer* (*Chelarctus cultrifer*), stage IV. A, ventral view; B, ventral view of eye, antennule and antenna; C, 2nd maxilla and 2nd maxilliped; D, 1st maxilla; E, ventral view of 5th pereiopod and abdomen; F, dorsal view of 5th pereiopod and abdomen. Parenthetic names are new genera and species names established by Holthuis (2002).

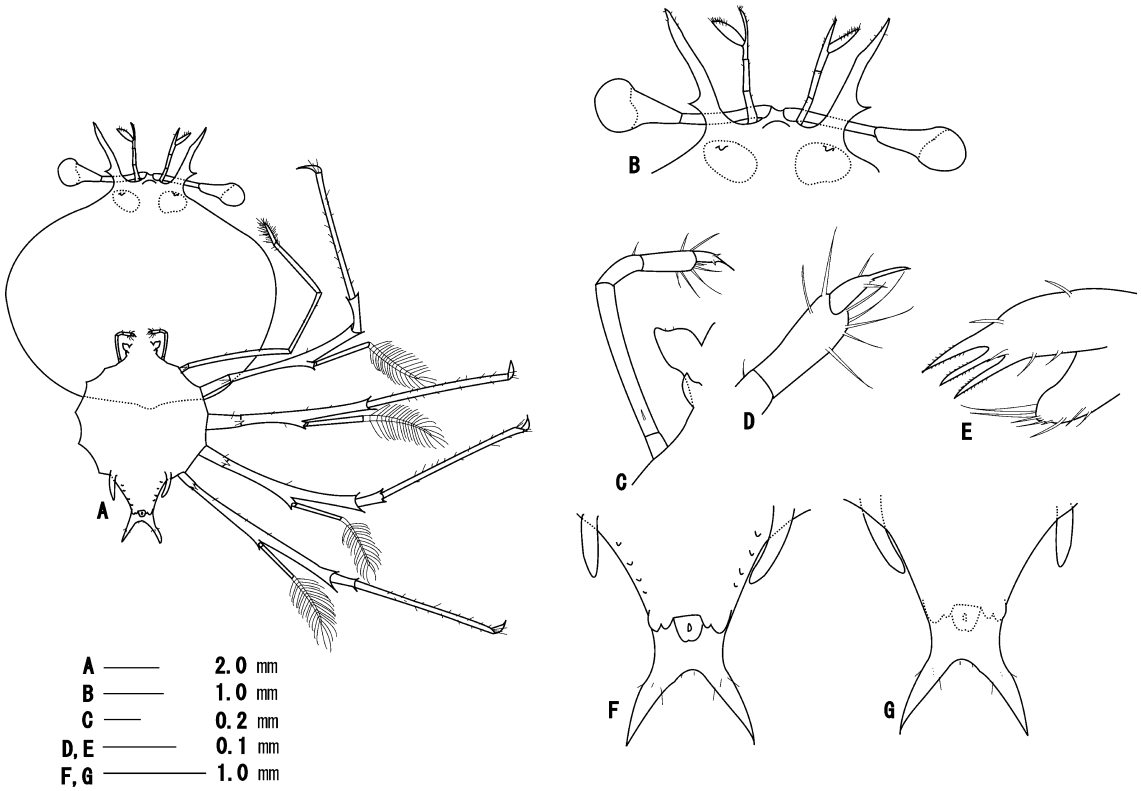

Fig. 12. Phyllosoma larva of *Scyllarus cultrifer* (*Chelarctus cultrifer*), stage V. A, ventral view; B, ventral view of eye, antennule and antenna; C, 2nd maxilla, 1st and 2nd maxilliped; D, distal end of 2nd maxilliped; E, 1st maxilla; F, ventral view of 5th pereiopod and abdomen; G, dorsal view of 5th pereiopod and abdomen. Parenthetic names are new genera and species names established by Holthuis (2002).

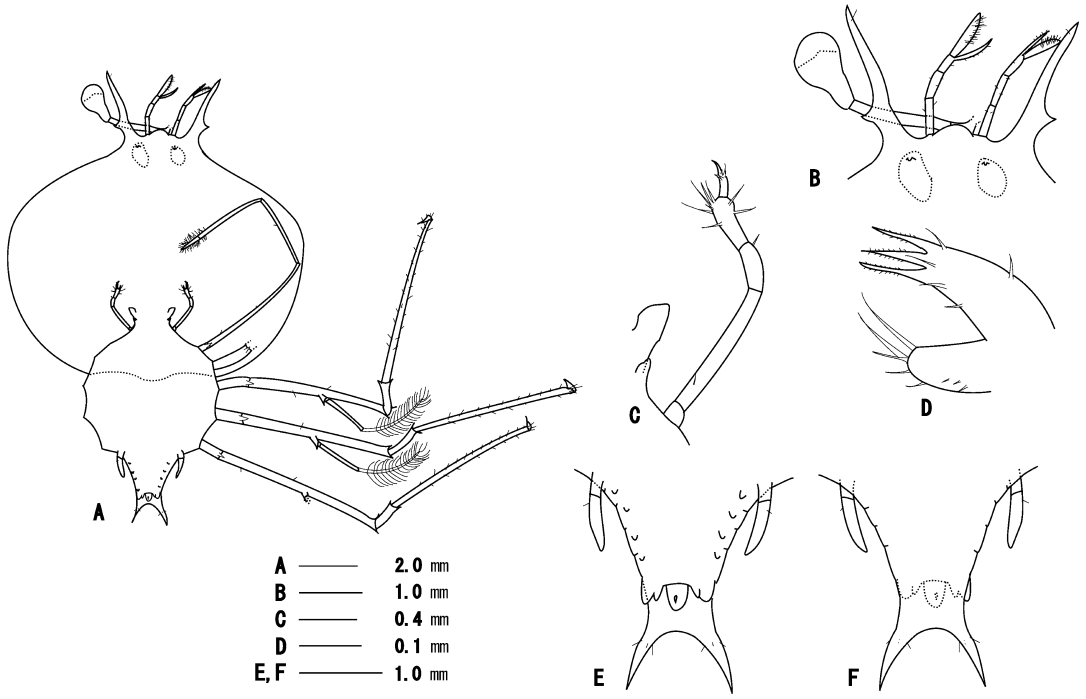

Fig. 13. Phyllosoma larva of *Scyllarus cultrifer* (*Chelarctus cultrifer*), stage VI. A, ventral view; B, ventral view of eye, antennule and antenna; C, 2nd maxilla, 1st and 2nd maxillipeds; D, 1st maxilla; E, ventral view of 5th pereiopod and abdomen; F, dorsal view of 5th pereiopod and abdomen. Parenthetic names are new genera and species names established by Holthuis (2002).

short setae, posterior lobe 6 short setae; 2nd maxilla (Fig. 12C) lobate bud. First appearance of 1st maxilliped (Fig. 12C) bud; 2nd maxilliped (Figs. 12C, D) bearing at least 3 setae on dactylus. Exopods of 1st to 4th pereiopods (Fig. 12A) bearing 17, 16, 14 and 15 pairs of natatorial setae, respectively; 5th pereiopod (Figs. 12F, G) elongated bud, much shorter than telson. Abdomen (Figs. 12F, G) slightly shorter than 1/2 of hindbody length; first appearance of pleopod and uropod buds (Fig. 12F); uropod (Fig. 12F) bud notched. Other characters as in stage IV.

Stage VI (Fig. 13)

BL (n=6), 11.5–13.5 mm (mean 12.6 mm); CL, 7.8–9.1 mm (mean 8.3 mm); CW, 9.6–11.0 mm (mean 10.2 mm); TW, 4.3–5.2 mm (mean 4.8 mm); CL/CW, 0.8 (mean 0.8); CW/TW, 2.0–2.3 (mean 2.1). Of these larval specimens, we described the morphological features of a larva (BL 12.6 mm) collected at 26°43.1′N, 133°19.5′E on June 16, 1984.

Antennule (Fig. 13B) outer flagellum bearing at least 20 minute setae on inner margin; antenna (Fig. 13B) with at least 1 minute seta. Second maxillipeds (Fig. 13C) with at least 8 setae on propodus. First pereiopod (Fig. 13A) damaged; exopods of 2nd and 3rd pereiopods (Fig. 13A) bearing 16 and 14 pairs of natatory setae, respectively; exopod of 4th pereiopod (Fig. 13A) damaged; 4th pereiopod (Figs. 13E, F) elongate bud with 2 segments bearing at least 1 minute seta. Other characters as in stage V.

Stage VII (Fig. 14)

BL (n=11), 15.3–18.3 mm (mean 16.5 mm); CL, 9.8–11.8 mm (mean 10.8 mm); CW, 15.0–17.3 mm (mean 13.3 mm); TW, 5.6–7.0 mm (mean 6.2 mm); CL/CW, 0.8 (mean 0.8); CW/TW, 2.1–2.2 (mean 2.2). Of these larval specimens, we described the morphological features of a larva (BL 15.3 mm) collected at 31°29.8′N, 129°59.6′E on Nov. 5, 1986.

Second maxilla (Fig. 14C) with developed scaphognathite lacking any seta. Second maxilliped (Figs. 14C, D) with rudiment of exopod appearing as slight protrusion, at least 11 setae on propodus and 5 setae on dactylus, respectively. Exopods of 1st to 3rd pereiopods (Fig. 14A) lost; 4th pereiopods (Fig. 14A) lost; 5th pereiopod (Figs. 14F, G) elongate, 3 segmented, lacking ventral coxal spine. Pleopods (Fig. 14F) bilobed; uropods (Fig. 14F) enlarged and biramous, beginning to be segmented. Other characters as in stage VI.

Stage VIII (final phyllosoma stage) (Fig. 15)

BL (n=30), 21.0–23.3 mm (mean 22.2 mm); CL, 12.2–14.0 mm (mean 13.2 mm); CW, 15.0–17.3 mm (mean 13.2 mm); TW, 7.3–8.7 mm (mean 8.0 mm); CL/CW, 0.8–0.9 (mean 0.8); CW/TW, 1.9–2.2 (mean 2.2). Of these larval specimens, we described the morphological features of a larva (BL 21.5 mm) collected at 26°43.1′N, 133°19.5′E on June 16, 1984.

First maxilla (Fig. 15E) posterior lobe bearing 3 short

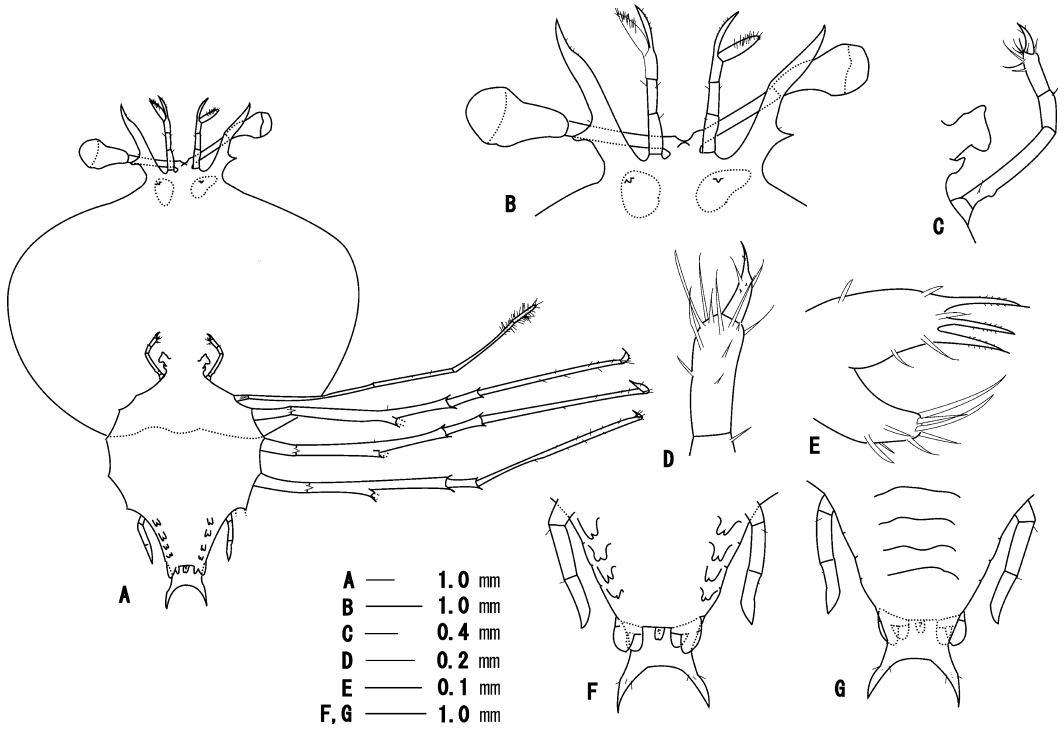

Fig. 14. Phyllosoma larva of *Scyllarus cultrifer* (*Chelarctus cultrifer*), stage VII. A, ventral view; B, ventral view of eye, antennule and antenna; C, 2nd maxilla, 1st and 2nd maxillipeds; D, distal end of 2nd maxilliped; E, 1st maxilla; F, ventral view of 5th pereiopod and abdomen; G, dorsal view of 5th pereiopod and abdomen. Parenthetic names are new genera and species names established by Holthuis (2002).

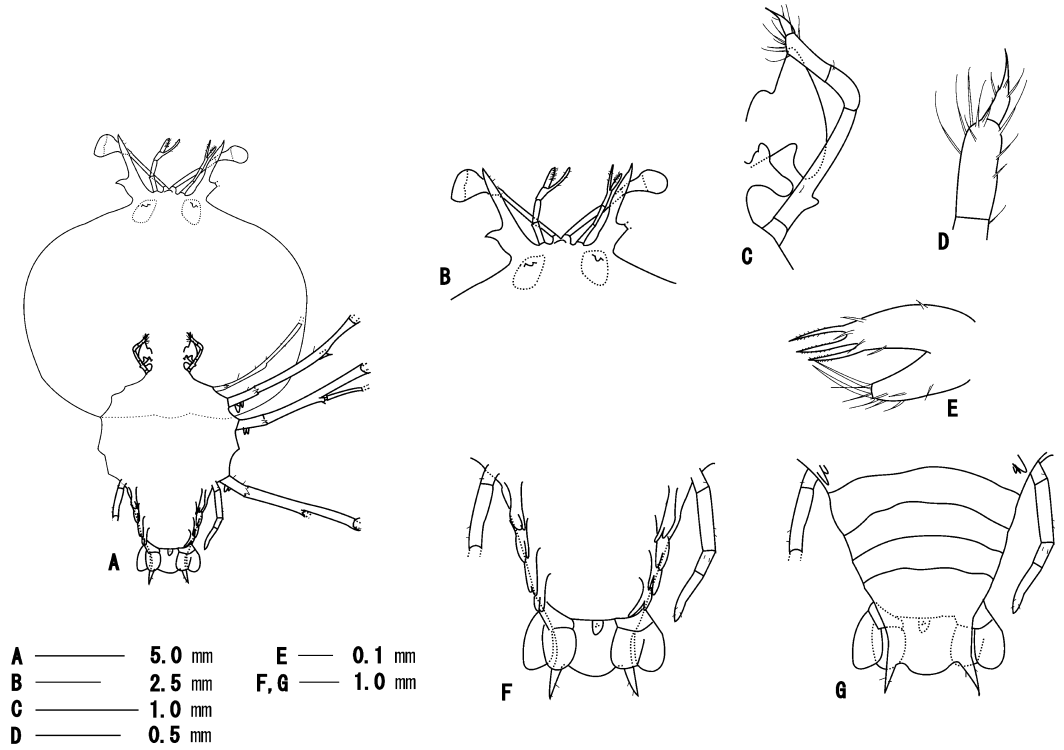

Fig. 15. Phyllosoma larva of *Scyllarus cultrifer* (*Chelarctus cultrifer*), stage VIII. A, ventral view; B, ventral view of eye, antennule and antenna; C, 2nd maxilla, 1st and 2nd maxillipeds; D, distal end of 2nd maxilliped; E, 1st maxilla; F, ventral view of 5th pereiopod and abdomen; G, dorsal view of 5th pereiopod and abdomen. Parenthetic names are new genera and species names established by Holthuis (2002).

Table 1. Characters distinguishing phyllosoma larvae of *Scyllarus bicuspidatus* (*Crenarctus bicuspidatus*) from those of *S. cultrifer* (*Chelarcthus cultrifer*).
Parenthetic names are new genus and species name revised by Holthuis (2002).

Stage		Body length (mm)	Antennule segment	Anterior lobe of 1st maxilla	Terminal setae of 2nd maxilla	1st maxilliped	Exopod of 4th pereiopod	5th pereiopod	Pleopod
IV	*S. bicuspidatus*	2.8–3.5	unsegmented	2 stout masticatory terminal spines	4 long terminal setae	lacking	bud	bud	lacking
	S. cultrifer	5.8–8.9	3-segmented	3 stout masticatory terminal spines	lacking	lacking	bearing 10 setal pairs	bud	lacking
V	*S. bicuspidatus*	3.6–4.9	2-segmented	3 stout masticatory terminal spines	4 long terminal setae	lacking	bearing 4 setal pairs	bud	bud
	S. cultrifer	9.4–11.1	3-segmented	3 stout masticatory terminal spines	lacking	bud	bearing 15 setal pairs	bud	bud
VI	*S. bicuspidatus*	5.1–7.3	3-segmented	3 stout masticatory terminal spines	lacking	bud	damaged	2-segmented, bearing ventral coxal spine	notched
	S. cultrifer	11.5–13.5	3-segmented	3 stout masticatory terminal spines	lacking	bud	damaged	2-segmented, lacking ventral coxal spine	bud
VII	*S. bicuspidatus*	8.2–10.2	3-segmented	3 stout masticatory terminal spines	lacking	bud	bearing 10 setal pairs	?-segmented, bearing ventral coxal spine	bilobed
	S. cultrifer	15.3–18.3	3-segmented	3 stout masticatory terminal spines	lacking	bud	damaged	3-segmented, lacking ventral coxal spine	bilobed
VIII	*S. bicuspidatus*	12.5–14.3	3-segmented	3 stout masticatory terminal spines	lacking	bud	bearing 11 setal pairs	4-segmented, bearing ventral coxal spine	biramous
	S. cultrifer	21.0–23.3	3-segmented	3 stout masticatory terminal spines	lacking	bud	damaged	4-segmented, lacking ventral coxal spine	biramous

terminal setae plus 5 short subterminal setae; 2nd maxilla (Fig. 15C) with more developed scaphognathite. First maxilliped (Fig. 15C) bilobate; 2nd maxilliped (Figs. 15C, D) bearing at least 11 setae on propodus; 3rd maxilliped (Fig. 15A) damaged, with rudiment of exopod appearing as slight protrusion. Pereiopods (Fig. 15A), except for 5th one, with gill-buds on coxal segment; 1st to 4th pereiopods difficult to observe due to damaged appendage; 5th pereiopod (Figs. 15F, G) elongate and 4 segmented, lacking ventral coxal spine. Abdomen (Figs. 15F, G) nearly 4 segmented; pleopods (Fig. 15F) biramous and unsegmented; uropods (Figs. 15F, G) enlarged and clearly segmented, protruding, not beyond telson; telson (Figs. 15F, G) with slight protrusion at distal margin between postero-lateral angles. Other characters as in stage VII.

Discussion

As compiled in Table 1, these two *Scyllarus* species are distinguishable at comparable stages by using a combination of body lengths and morphological characteristics of the antennule, pereiopods and pleopods. In addition, a) *S. cultifer* is always larger than *S. bicuspidatus*; b) the cephalic shield of *S. bicuspidatus* is rounder than *S. cultrifer*; c) relative to antennule length, the eyestalk is longer in *S. cultrifer* than in *S. bicuspidatus*. Then, as compiled in Table 2, phyl-

Table 2. Identification key for phyllosoma stages of *Scyllarus bicuspidatus* and *S. cultrifer*.
Parenthetic names are new genus and species name revised by Holthuis (2002).

***Scyllarus bicuspidatus* (*Crenarctus bicuspidatus*)**	
(1) Eye stalk unsegmented; 4th pereiopod absent	Stage I
Eye stalk segmented; 4th pereiopod present	(2)
(2) Fourth pereiopod bud, lacking ventral coxal spine	Stage II
Fourth pereiopod developed, bearing ventral coxal spine	(3)
(3) Fourth pereiopod unsegmented	Stage III
Fourth pereiopod segmented	(4)
(4) Pleopods lacking; antennule unsegmented	Stage IV
Pleopods bearing; antennule segmented	(5)
(5) Antennule 2-segmented; pleopod buds unnotched; 5th pereiopod unsegmented	Stage V
Antennule 3-segmented; pleopod buds notched; 5th pereiopod 2-segmented	(6)
(6) Pleopod buds notched	Stage VI
Pleopod buds bilobed	(7)
(7) Pereiopods lacking gill-buds on coxal segment	Stage VII
Pereiopods bearing gill-buds on coxal segment	Stage VIII (final)

***Scyllarus cultrifer* (*Chelarcthus cultrifer*)**	
(1) Pleopods absent	Stage IV
Pleopods present	(2)
(2) Fifth pereiopod unsegmented	Stage V
Fifth pereiopod 2-segmented	(3)
(3) Pleopod buds unnotched	Stage VI
Pleopod buds bilobed	(4)
(4) Pereiopods lacking gill-buds on coxal segment	Stage VII
Pereiopods bearing gill-buds on coxal segment	Stage VIII (final)

Table 3. Key to the species of late-stage *Scyllarus* phyllosoma larvae in Japan and its neighbouring waters (updated to date).
Modified from Sekiguchi & Inoue (2002).
Parenthetic names are new genus and species name revised by Holthuis (2002).

(1) Cephalic shield more or less trapezoidal in shape	(2)
Cephalic shield oval or round	(3)
(2) Distal end of uropod pointed	*S. martensii* (*Eduarctus martensii*)
Distal end of uropod not pointed	*S. aurora* (*Galearctus aurora*)
(3) Telson extending beyond uropod, with two prominent posteriorly directed lateral spines	(4)
Telson not extending beyond uropod	(5)
(4) Lateral process of antenna directed laterally	*S. cultrifer* (*Chelarctus cultrifer*)
Lateral process of antenna directed laterally; cephalic shield with higher width ratio to different parts of the body than *S. cultrifer*; 5th pereiopod bearing ventrally-directed coxal spines	*Scyllarus* sp. d
Lateral process of antenna directed anteriorly	*S. bicuspidatus* (*Crenarctus bicuspidatus*)
Lateral process of antenna directed anteriorly; cephalic shield more rounded and eyestalk much shorter than *S. bicuspidatus*	*Scyllarus* sp. e
(5) Eyestalk longer than antennule; lateral process of antenna directed anteriorly	*S. kitanoviriosus* (*Galerctus kitanoviriosus*)
Eyestalk nearly equal length to or shorter than antennule	(6)
(6) Lateral process of antenna directed laterally	*S. rugosus* (*Petrarctus rugosus*)
Lateral process of antenna directed anteriorly	*Scyllarus* sp. c

losoma larvae of these two *Scyllarus* species can be identified to stages using a combination of morphological features of the eyestalk, fourth and fifth pereiopods, pleopods and gill-buds.

According to Sekiguchi's (1986a) key for identification, late-stage phyllosoma larvae of *S. bicuspidatus* identified in the present study are identical with *Scyllarus* sp. a, based on the shape of the lateral process of the antennae (directed anteriorly), while late-stage phyllosoma larvae of *S. cultrifer* identified in the present study are identical with *S. bi-*

cuspidatus based on the shape of the lateral process of the antennae (directed laterally). Furthermore, according to detailed comparisons of phyllosoma specimens loaned from Dr. Matsuda (Mie Prefectural Science and Technology Promotion Center, pers. comm.) who succeeded in culturing from eggs to nisto larvae of *S. bicuspidatus* and *S. cultrifer* in the laboratory (see Inoue et al. 2000), *Scyllarus* sp. a and *S. bicuspidatus* in Sekiguchi's (1986a) key were actually identifiable as *S. bicuspidatus* and *S. cultrifer* (see Higa & Shokita 2004), respectively.

Saisho (1964) and Konishi & Sekiguchi (1990) described stage I phyllosoma larvae of *S. bicuspidatus* and *S. cultrifer* hatched in the laboratory. According to the present study, as well as the above studies, the cephalon of *S. cultrifer* phyllosoma larvae did not reach the base of the third maxilliped, while that of *S. bicuspidatus* did. Judging from this, it is no problem to separate phyllosoma larvae of the above two *Scyllarus* species. Judging from the morphological features of the cephalon, stage I phyllosoma larvae of *S. bicuspidatus* in the present study are identical with those of the same species described by Saisho (1964). However, between the stage I phyllosoma larvae described by Saisho (1964) and the present study, antennule shape differed slightly, because the phyllosoma larvae of Saisho (1964) and the present study probably belonged to a different instar of stage I.

Morphological features of *S. cultrifer* phyllosoma larvae identified in the present study accord well with those of *S. bicuspidatus* described by Phillips et al. (1981) from the south-eastern Indian Ocean, *Scyllarus* sp. a as described by Johnson (1971a) from the South China Sea, and *S. bicuspidatus* described by Sekiguchi (1990) from Mariana waters. Adults of *S. cultrifer* have also been reported in the neighboring waters of the South China Sea and Mariana waters (Chan & Yu 1986), but not from the south-eastern Indian Ocean (Phillips et al. 1981). Judging from these data, phyllosoma larvae of *Scyllarus* sp. a described by Johnson (1971a) and *S. bicuspidatus* described by Sekiguchi (1990) are thought to have been *S. cultrifer*. *Scyllarus* sp. A phyllosoma larvae from the northwest shelf of Australia were described and were referred to as *S. cultrifer* or others (*S. kitanoviriosus*, *S. umbilicatus* or *S. timidus*) by McWilliam et al. (1995). However, the morphological features of *Scyllarus* sp. A clearly differ from those of both *S. bicuspidatus* and *S. cultrifer* phyllosoma larvae identified in the present study: very long eyestalk, and telson not extending beyond uropods in *S. cultrifer*. The *S. bicuspidatus* phyllosoma larvae described by Phillips et al. (1981) from the south-eastern Indian Ocean may also not be this species. On the other hand, *Scyllarus* sp. b described by Phillips et al. (1981) from the south-eastern Indian Ocean accords well with *S. bicuspidatus*, except for lacking a ventral coxal spine on the basal segment of the fifth pereiopod. *S. cultrifer* has not been reported from the western Australian waters. According to Holthuis (2002), *S. bicuspidatus* is most closely-related to *S. crenatus* (*Crenarctus crenatus* in Holthuis' (2002) revision). Therefore their larvae and nistos would probably bear close resemblances. As *S. crenatus* adults have been recorded mainly from the New South Wales coast of eastern Australian waters (Holthuis 2002), we suspect that this is more likely (than *S. bicuspidatus*) to be the real identity of the numerically dominant scyllarid species in McWilliam & Phillips (1983).

Of the 11 *Scyllarus* species known from Japan and its neighboring waters, the morphological features of late-stage phyllosoma larvae all but four species (*S. bertholdii*, *S. brevicornis*, *S. formosanus* and *S. longidactilus*) have been described: *S. aurora* (not *S. timidus*) by Johnson (1971b), *S. batei* by Prasad et al. (1975), *S. bicuspidatus* and *S. cultrifer* by Inoue et al. (2000, 2001), *S. cultrifer* by Higa & Shokita (2004), *S. kitanoviriosus* by Higa & Saisho (1983), *S. martensii* by Phillips & McWilliam (1986), and *S. rugosus* by Berry (1974) and Prasad et al. (1975). Based on the previous studies and his-own description, Sekiguchi (1986a) distinguished late-stage phyllosoma larvae of six *Scyllarus* species, i.e. *S. aurora*, *S. bicuspidatus* (=*S. cultrifer* in Inoue et al. (2001) and also in the present study), *S. cultrifer* (=*Scyllarus* sp. c in Inoue et al. (2001)), *S. kitanoviriosus*, *S. martensii*, and *Scyllarus* sp. a (*S. bicuspidatus* in Inoue et al. (2001) and also in the present study and not identical to *Scyllarus* sp. a in Johnson (1971a)). In addition to late-stage phyllosoma larvae of the above seven *Scyllarus* species, based on field-caught specimens, Inoue et al. (2001) described and distinguished late-stage phyllosoma larvae of two *Scyllarus* species (*Scyllarus* sp. d and *Scyllarus* sp. e) not yet referrable to known adult species. It is possible now to separate and identify phyllosoma larvae of *S. bicuspidatus* and *S. cultrifer* from those of nine *Scyllarus* species (Table 3), based on Sekiguchi (1986a), Inoue et al. (2001) and information from the present study.

Acknowledgements

We wish to express our sincere thanks to Messrs Y. Nishikawa (National Research Institute of Far Seas Fisheries) and T. Nagasawa (Japan Sea National Research Institute) for giving us the opportunity to examine ichthyoplankton samples used in the present study. Thanks are due to Ms Paulette S. McWilliam for her comments on an early version of our manuscript, and to Dr. H. Matsuda (Mie Prefectural Science and Technology Promotion Center) for his personal communication cited in the present study. Thanks are also extended to the captain and crew of the vessels (Mizunagi-Maru, Mizuho-Maru, Syoyo-Maru, Wakashio-Maru and Ootori-Maru) for the on board sampling.

References

Berry PF (1974) Palinurid and scyllarid lobster larvae of the Natal coast, South Africa. Invest Rep Oceanogr Res South Africa 34: 1–44.

Booth JD, Phillips BF (1994) Early life history of spiny lobster. Crustaceana 66: 271–294.

Booth JD, Webber WR, Sekiguchi H, Coutures E (2005) Diverse larval recruitment strategies within the Scyllaridae. New Zealand J Mar Freshwat Res 39: 581–592.

Chan TY, Yu HP (1986) A report of the *Scyllarus* lobsters (Crustacea: Dcapoda: Scyllaridae) from Taiwan. J Taiwan Mus 39: 147–174.

Higa T, Saisho T (1983) Metamorphosis and growth of the late-stage phyllosoma of *Scyllarus kitanoviriosus* Harada (Decapoda, Scyllaridae). Mem Kagoshima Univ Res Center South Pacific 3: 86–98. (in Japanese)

Higa T, Shokita S (2004) Late-stage phyllosoma larvae and metamorphosis of a scyllarid lobster, *Chelarctus cultrifer* (Crustacea: Decapoda: Scyllaridae), from the northwestern Pacific. Species Diversity 9: 221–250.

Holthuis LB (2002) The Indo-Pacific scyllarine lobsters (Crustacea, Decapoda, Scyllaridae). Zoosystema 24: 499–693.

Inoue N, Sekiguchi H (2001) Distribution of late-stage phyllosoma larvae of *Panulirus japonicus* in the Kuroshio Subgyre. Mar Freshwat Res 52: 1201–1209.

Inoue N, Sekiguchi H (2005) Distribution of scyllarid phyllosoma larvae (Crustacea: Decapoda: Scyllaridae) in the Kuroshio Subgyre. J Oceanogr 61: 389–398.

Inoue N, Sekiguchi H, Nagasawa T (2000) Distribution and identification of phyllosoma larvae in the Tsushima Current region. Bull Japan Soc Fish Oceanogr 64: 129–137. (in Japanese)

Inoue N, Sekiguchi H, Yeh SP (2001) Spatial distributions of phyllosoma larvae (Crustacea: Decapoda: Palinuridae and Scyllaridae) in Taiwanese waters. J Oceanogr 57: 535–548.

Inoue N, Minami H, Sekiguchi H (2004) Distribution of phyllosoma larvae (Crustacea: Decapoda: Palinuridae, Scyllaridae and Synaxidae) in the western North Pacific. J Oceanogr 60: 963–976.

Ito M, Lucas JS (1990) The complete larval development of the scyllarid lobster, *Scyllarus demani* Holthuis, 1946 (Decapoda, scyllaridae), in the laboratory. Crustaceana 58: 144–167.

Johnson MW (1971a) On palinurid and scyllarid lobster larvae and their distribution in the South China Sea (Decapoda, Palinuridea). Crustaceana 21: 247–282.

Johnson MW (1971b) The phyllosoma larvae of slipper lobsters from the Hawaiian Islands and adjacent areas. Crustaceana 20: 77–103.

Konishi K, Sekiguchi H (1990) First-stage phyllosoma of *Scyllarus cultrifer* (ORTMANN) (Decapoda, Scyllaridae). Bull. Plankton Soc Japan 37: 77–82.

McWilliam PS, Phillips BF (1983) Phyllosoma larvae and other macroplankton associated with Eddy J, a warm-core eddy off south-eastern Australia. Aust J Mar Freshwat Res 34: 653–661.

McWilliam PS, Phillips BF, Kelly S (1995) Phyllosoma larvae of *Scyllarus* species (Decapoda, Scyllaridae) from the shelf waters of Australia. Crustaceana 68: 537–566.

Phillips BF, Brown PA, Rimmer DW, Brain SJ (1981) Description, distribution and abundance of late larval stages of the Scyllaridae (slipper lobster) in the south-eastern Indian Ocean. Aust J Mar Freshwat Res 32: 412–437.

Phillips BF, McWilliam MC (1986) Phyllosoma and nisto stage of *Scyllarus martensii* Pfeffer (Decapoda, Scyllaridae) from the Gulf of Carpentaria, Australia. Crustaceana 51: 133–154.

Prasad RR, Tampi PRS, George MJ (1975) Phyllosoma larvae from the Indian Ocean collected by the DANA Expedition 1928–1930. J Mar Biol Ass India 17: 56–107.

Robertson PB (1968) The complete larval development of the sand lobster, *Scyllarus americanus* (Smith), (Decapoda, Scyllaridae) in the laboratory, with note on larvae from the plankton. Bull Mar Sci 18: 294–342.

Saisho T (1964) Notes on the first stage phyllosoma of scyllarid lobster, *Scyllarus bicuspidatus*. Mem Fac Fish Kagoshima Univ 13: 1–4.

Sekiguchi H (1986a) Identification of late-stage phyllosoma larvae of the scyllarid and palinurid lobster in the Japanese waters. Bull Japan Soc Sci Fish 52: 1289–1294.

Sekiguchi H (1986b) Spatial distribution and abundance of phyllosoma larvae in the Kumano- and Enshu-nada Seas north of the Kuroshio Current. Bull Japan Soc Fish Oceanogr 50: 289–297.

Sekiguchi H (1990) Four species of phyllosoma larvae from the Mariana waters. Bull Japan Soc Fish Oceanogr 54: 242–248.

Sekiguchi H, Inoue N (2002) Recent advances in larval recruitment processes of scyllarid and palinurid lobsters in Japanese waters (a review). J Oceanogr 58: 747–757.

Wada Y, Kawahara A, Munekiyo M, Sobajima N (1985) Distribution and larval stages of the phyllosoma larvae of a scyllarid lobster, *Scyllarus kitanoviriosus*, in the western Wakasa Bay. Bull Kyoto Oceanogr Fish Sci 9: 51–57. (in Japanese)