

## Larval development of *Brachynotus sexdentatus* (Risso, 1827) (Decapoda, Brachyura) reared under laboratory conditions, with notes on larval characters of the Varunidae

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### Summary

The complete larval development of *Brachynotus sexdentatus* (Risso, 1827) was obtained by culture in the laboratory. Five zoeal stages, megalop and first crab are described and illustrated. Larval development from hatching to megalop stage took a minimum of 17 days at 23°C. The morphological characters of the larvae of *B. sexdentatus* are compared with those of the previous descriptions of plankton-collected material and other known larvae of the genus *Brachynotus*. Larval features of the recently redefined Varunidae are evaluated taking into account all previous larval descriptions from this family. A combination of consistent characters can be used to distinguish varunid zoeas and megalops stages from the early life stages of all other grapsoid families.

**Key words:** *Brachynotus sexdentatus*, Varunidae, Grapsoidea, zoea, megalop, larval development

### Introduction

Four species of *Brachynotus* are known from northeast Atlantic and Mediterranean waters: *B. atlanticus* Forest, 1957; *B. foresti* Zariquiey Álvarez, 1968; *B. gemmellari* (Rizza, 1839); and *B. sexdentatus* (Risso, 1827) (d'Udekem d'Acoz, 1999). These crabs are representatives of the marine intertidal and shallow subtidal. Detailed descriptions of the complete larval development are only available for *B. atlanticus* (see Rodríguez et al., 1992) and *B. gemmellari* (see Guerao

et al., 1995). In addition, incomplete knowledge exists on the larval development of *B. sexdentatus* from plankton-collected material (Bourdillon-Casanova, 1960; Paula, 1987). *B. gemmellari* was resurrected by Froggia and Manning (1978) based on differences in morphometry and habitat from *B. sexdentatus*. But genetic identity in 16S mitochondrial DNA sequence of *B. gemmellari* and *B. sexdentatus* suggests a very close relationship or synonymy of these two species (Schubart et al., in press).

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The acceptance of the Varunidae as a brachyuran family (see Guinot, 1977, 1978) is based on recent results of molecular phylogenetics (Schubart et al., 2000) and larval morphology (Cuesta, 1999). The taxa comprising the Varunidae differ from the traditional grapsid subfamily Varuninae (*sensu* Balss, 1957) by exclusion of the genera *Euchirograpsus* (see Cuesta and Schubart, 1997; d'Udekem d'Acoz, 1999), *Glyptograpsus* and *Platychirograpsus* (see Schubart and Cuesta, submitted) and by inclusion of the former sesarmine genera *Chasmagnathus*, *Cyclograpsus*, *Helice*, *Helograpsus*, *Metaplax* and *Paragrapsus* (see Schubart and Cuesta, 1998; Cuesta, 1999; Schubart et al., 2000). In terms of the number of genera (23), the Varunidae rank first within the Grapsoidea and in terms of the number of species (108) second behind the Sesarmidae. Larval data of Varunidae are known from 14 genera (39 species) gathered in 62 publications (see appendix). Presently, there are no larval data available for the genera *Heterograpsus*, *Orcovita*, *Pseudograpsus*, *Ptychognathus*, *Pyxidognathus*, *Scutumara*, *Tetragrapsus*, *Utica*, and *Xenograpsus*.

In the present paper, the larval development of *B. sexdentatus* is described and illustrated, and larval morphology is compared with the one of other species known from this genus, especially the phylogenetically close *B. gemmellari*. Furthermore, the 62 published papers dealing with larval data of varunids are analyzed, and a list of larval characters is proposed as typical and distinctive for Varunidae.

### Materials and Methods

Males and females of *B. sexdentatus* were collected in a marine fish culture pond (36 PSU) at Puerto Santa María (Cádiz, Spain) on March 11, 1994. The sample was taken by hand when the pond was dried. The bottom (1–2-m deep) was muddy. Identification of adult crabs was carried out by Antonio Rodríguez and based on the key of Frogliia and Manning (1978). Three ovigerous crabs, transported to the laboratory at the Instituto de Ciencias Marinas de Andalucía (CSIC), were maintained in aquaria containing natural seawater until the eggs hatched (March 12, 14, 18, 1994). The larvae were transferred to beakers of 2-l capacity for mass culture. Natural seawater was used at a temperature of 23±1°C and salinity of 32 PSU. Larvae were subjected to continuous artificial light regime: 8/16 h (L/D). First to third zoeal stages were reared and fed with rotifers *Brachionus plicatilis*. Zoea IV to V and megalop were fed with newly hatched nauplii of *Artemia* sp. offered *ad libitum*.

Drawings and measurements were made using a Wild MZ6 and Olympus BH compound microscope, both equipped with a *camera lucida*. All measurements were made using an ocular micrometer. Semi-permanent mounts were made of whole larvae and dissected appendages were stained using CMC10 (Turtox Ltd.) and lignin pink. Drawings were based on five larvae, and measurements on 10 larvae per stage. In zoeal stages, rostro-dorsal length (rdl) was measured from the tip of the rostral spine to the tip of the dorsal spine; carapace length (cl) from the base of the rostrum to the posterior margin; carapace width (cw) as the distance between the tips of the lateral spines. In the megalopal stage, carapace length (cl) was measured from the base of the rostrum to the posterior margin and carapace width (cw) as the maximum width. The long natatory setae on the distal exopod segments of the first and second maxillipeds are drawn truncated in Figs. 7 and 8. Also, long aesthetascs of the antennules are truncated in the Fig. 3. Description and figures are arranged according to the standard proposed by Clark et al. (1998).

Samples of larvae (zoea I to megalop) and several adult males and females of *B. sexdentatus* were deposited at the Museo Nacional de Ciencias Naturales de Madrid (Spain) under the accession number MNCN 20.04/4637.

### Results

The complete larval development of *B. sexdentatus* took place through five zoeal stages and a megalop. It was completed in a minimum of 17 days from hatching. First crab stage was reached at 22 days from hatching. Mean sizes (rdl, cw and cl), first day of appearance, and duration of each stage are presented in Table 1.

### Description of *Brachynotus sexdentatus* (Risso, 1827)

Previous descriptions: Zoea I, Bourdillon-Casanova, 1960: 182, Fig. 58. Zoea II, Paula, 1987: 735, Fig. 12. Zoea III, Bourdillon-Casanova, 1960: 182, Fig. 58. Zoea IV, Bourdillon-Casanova, 1960: 183, Fig. 58. Zoea V, Bourdillon-Casanova, 1960: 184, Fig. 58; Paula, 1987: 737, Fig. 13. Megalop, Bourdillon-Casanova, 1960: 184, Fig. 59. First crab, Bourdillon-Casanova, 1960: 185, Fig. 60.

Table 1. Measurements (rostrum-dorsal length, carapace width and carapace length) of the larvae and first crab of *Brachynotus sexdentatus* (mean  $\pm$ SD) in mm, first day of appearance and duration of each stage

|            | rdl                | cw                 | cl                 | First day of appearance | Duration (days) |
|------------|--------------------|--------------------|--------------------|-------------------------|-----------------|
| Zoea I     | 1.35 ( $\pm$ 0.04) | 0.59 ( $\pm$ 0.02) | 0.49 ( $\pm$ 0.01) | 0                       | 3               |
| Zoea II    | 1.71 ( $\pm$ 0.05) | 0.65 ( $\pm$ 0.01) | 0.58 ( $\pm$ 0.01) | 3                       | 4               |
| Zoea III   | 2.17 ( $\pm$ 0.07) | 0.79 ( $\pm$ 0.01) | 0.74 ( $\pm$ 0.02) | 6                       | 4               |
| Zoea IV    | 2.50 ( $\pm$ 0.05) | 1.01 ( $\pm$ 0.03) | 0.95 ( $\pm$ 0.04) | 9                       | 3               |
| Zoea V     | 3.35 ( $\pm$ 0.01) | 1.39 ( $\pm$ 0.04) | 1.17 ( $\pm$ 0.04) | 12                      | 5               |
| Megalop    | —                  | 1.43 ( $\pm$ 0.02) | 1.69 ( $\pm$ 0.02) | 17                      | 5               |
| First crab | —                  | 1.71 ( $\pm$ 0.02) | 1.55 ( $\pm$ 0.03) | 22                      | —               |

### Zoea I

*Carapace* (Fig. 1A). Globose, smooth and without tubercles. Dorsal and rostral spines long and straight. Lateral spines well developed. A pair of posterodorsal setae. Anterodorsal region, posterior and ventral margin without setae. Ventral margin with 4–5 denticles. Eyes sessile.

*Antennule* (Fig. 3A). Uniramous. Endopod absent. Exopod unsegmented with 3 aesthetascs (2 long, 1 thin and short) and 1 seta.

*Antenna* (Fig. 4A). Protopod less than half the length of the rostral spine and bearing two rows of spines. Exopod subequal in length to protopod and with 2 medial spines.

*Mandible*. Endopod palp absent.

*Maxillule* (Fig. 5A). Coxal endite with 5 plumodenticulate setae. Basial endite with 5 setae (2 cuspidate and 3 plumodenticulate). Endopod 2-segmented with 1 plumodenticulate seta on the proximal segment and 1 subterminal and 4 terminal plumodenticulate setae on the distal segment. Exopod seta absent. Epipod seta absent.

*Maxilla* (Fig. 6A). Coxal endite bilobed with 3+3 plumodenticulate setae. Basial endite bilobed with 5+4 plumodenticulate setae. Endopod unsegmented, bilobed with 2 long plumodenticulate setae on each lobe. Scaphognathite with 4 plumose marginal setae and a long setose posterior process.

*First maxilliped* (Fig. 7A). Coxa with 1 seta. Basis with 10 medial setae arranged 2,2,3,3. Endopod 5-segmented with 2,2,1,2,5 (1 subterminal + 4 terminal) setae. Exopod 2-segmented, distal segment with 4 natatory setae.

*Second maxilliped* (Fig. 8A). Coxa without setae. Basis with 4 medial setae arranged 1,1,1,1. Endopod 3-segmented with 0,1,6 (3 subterminal + 3 terminal) setae. Exopod 2-segmented, distal segment with 4 natatory setae.

*Third Maxilliped*. Absent.

*Pereiopods*. Absent.

*Abdomen* (Fig. 11A). Five abdominal somites. Somites 2 and 3 with a pair of dorsolateral processes. Somites 2–4 with a pair of posterodorsal setae. Pleopods absent.

*Telson* (Fig. 11A). Telson bifurcated with 3 pairs of serrulate setae on its posterior margin. In the inner distal part of each furcal arm a row of teeth, 4 terminal longer than the rest.

### Zoea II

*Carapace* (Fig. 1B). One pair of simple setae on the middle part of the dorsal spine. One pair of anterodorsal setae. Each ventral margin with 1 plumodenticulate anterior seta. Eyes stalked. Otherwise unchanged.

*Antennule* (Fig. 3B). Exopod with 1 additional aesthetasc. Otherwise unchanged.

*Antenna* (Fig. 4B). Unchanged.

*Mandible*. Unchanged.

*Maxillule* (Fig. 5B). Basial endite with 7 setae (2 plumodenticulate cuspidate and 5 plumodenticulate). Exopod seta present. Otherwise unchanged.

*Maxilla* (Fig. 6B). Coxal endite bilobed with 3+5 plumodenticulate setae. Scaphognathite with 8 plumose marginal setae, long posterior process reduced to normal size. Otherwise unchanged.

*First maxilliped* (Fig. 7B). Exopod 2-segmented, with 6 natatory setae. Otherwise unchanged.

*Second maxilliped*. Exopod 2-segmented, with 6 natatory setae. Otherwise unchanged.

*Third maxilliped*. Absent.

*Pereiopods*. Absent.

*Abdomen* (Fig. 11B). First somite with 1 long mid-dorsal seta. Otherwise unchanged.

*Telson* (Fig. 11B). Unchanged.

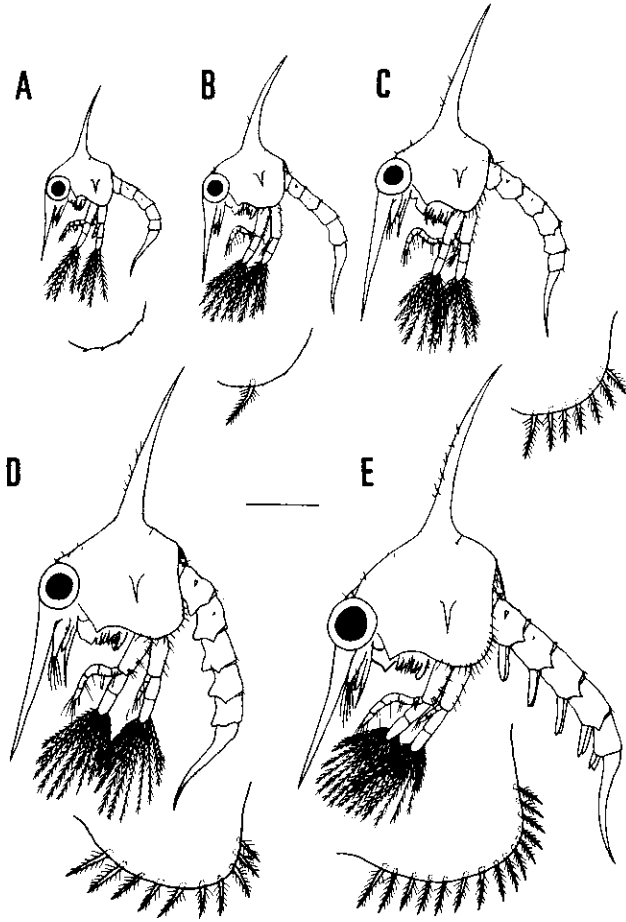


Fig. 1. *Brachynotus sexdentatus* (Risso), lateral view and magnification of ventral margin. A, zoea I; B, zoea II; C, zoea III; D, zoea IV; E, zoea V. Scale bar = 0.5 mm.

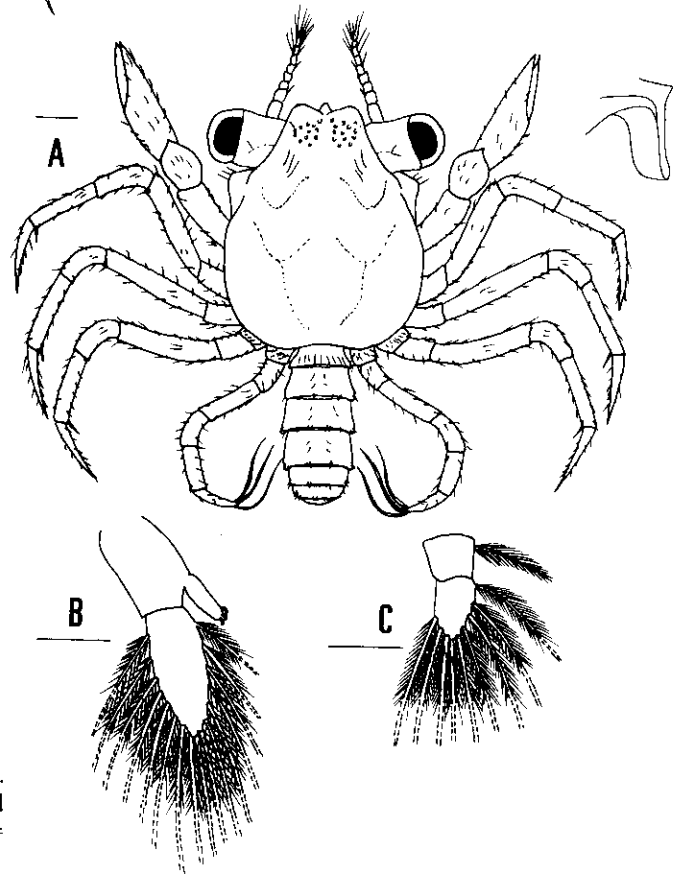


Fig. 2. *Brachynotus sexdentatus* (Risso), megalop. A, dorsal view and lateral view of rostrum; B, second pleopod; C, uropod. Scale bars, A= 0.3 mm, B,C= 0.1 mm.

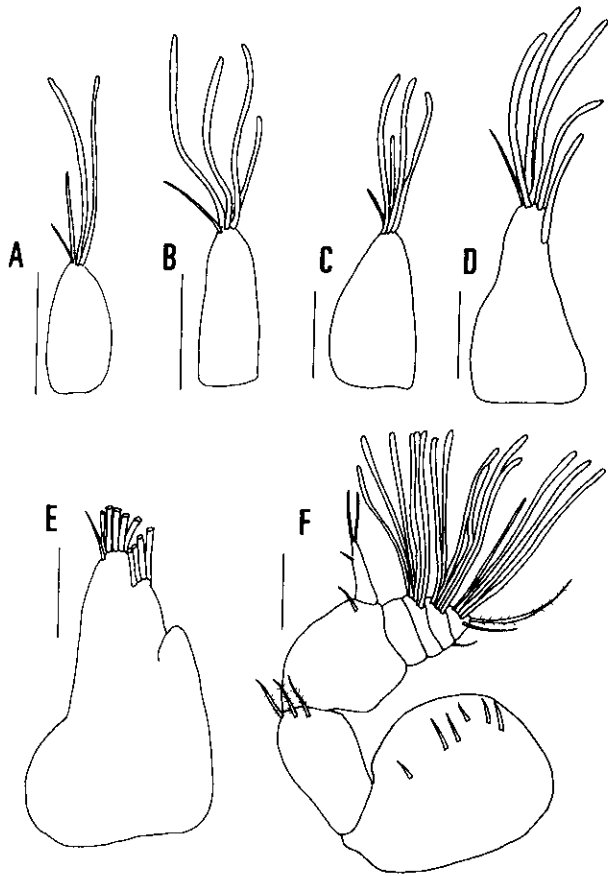


Fig. 3. *Brachynotus sexdentatus* (Risso), antennule. A, zoea I; B, zoea II; C, zoea III; D, zoea IV; E, zoea V; F, megalop. Scale bars = 0.1 mm.

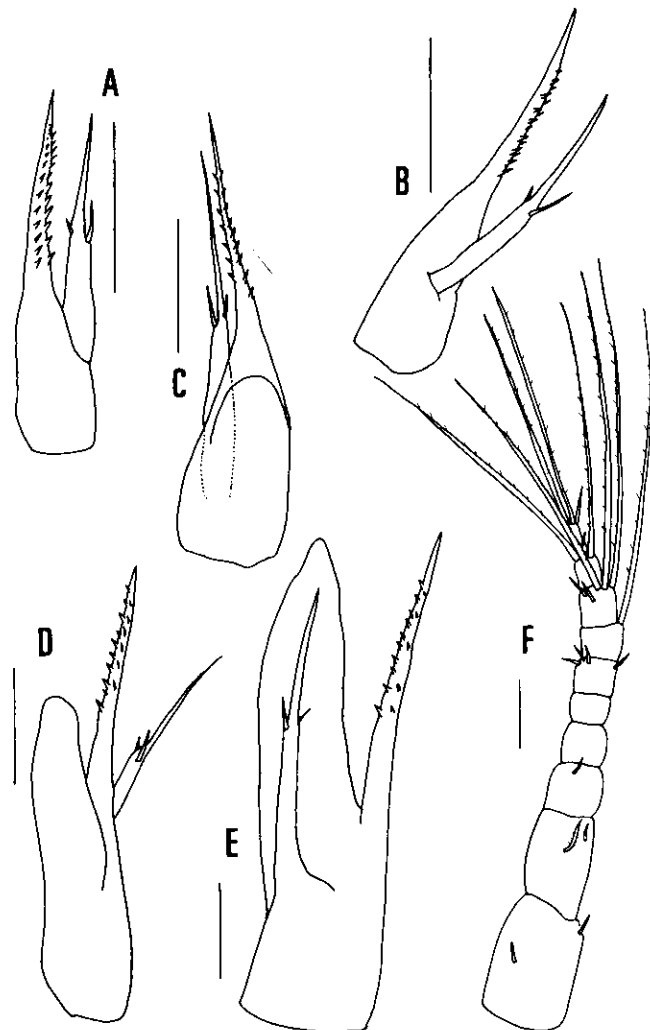


Fig. 4. *Brachynotus sexdentatus* (Risso), antenna. A, zoea I; B, zoea II; C, zoea III; D, zoea IV; E, zoea V; F, megalop. Scale bars = 0.1 mm.

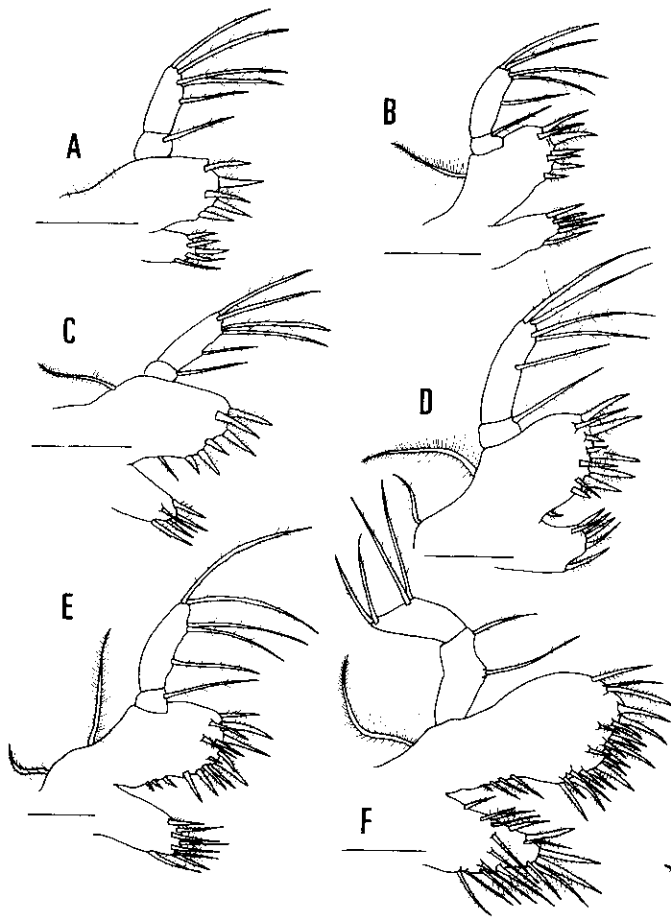


Fig. 5. *Brachynotus sexdentatus* (Risso), maxillule. A, zoea I; B, zoea II; C, zoea III; D, zoea IV; E, zoea V; F, megalop. Scale bars = 0.1 mm.

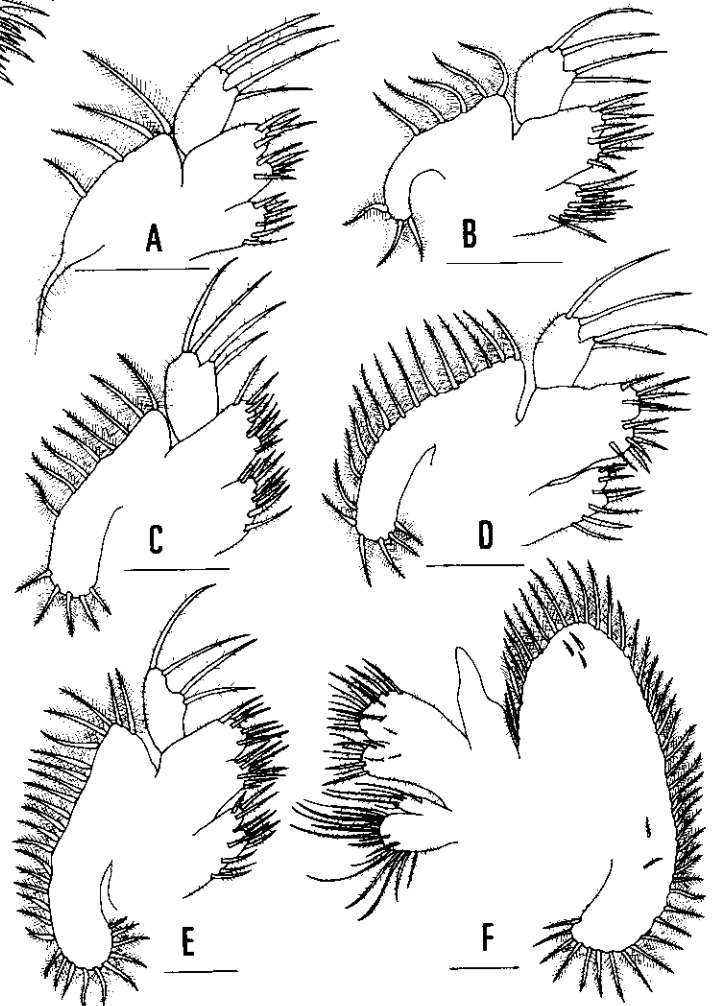


Fig. 6. *Brachynotus sexdentatus* (Risso), maxilla. A, zoea I; B, zoea II; C, zoea III; D, zoea IV; E, zoea V; F, megalop. Scale bars = 0.1 mm.

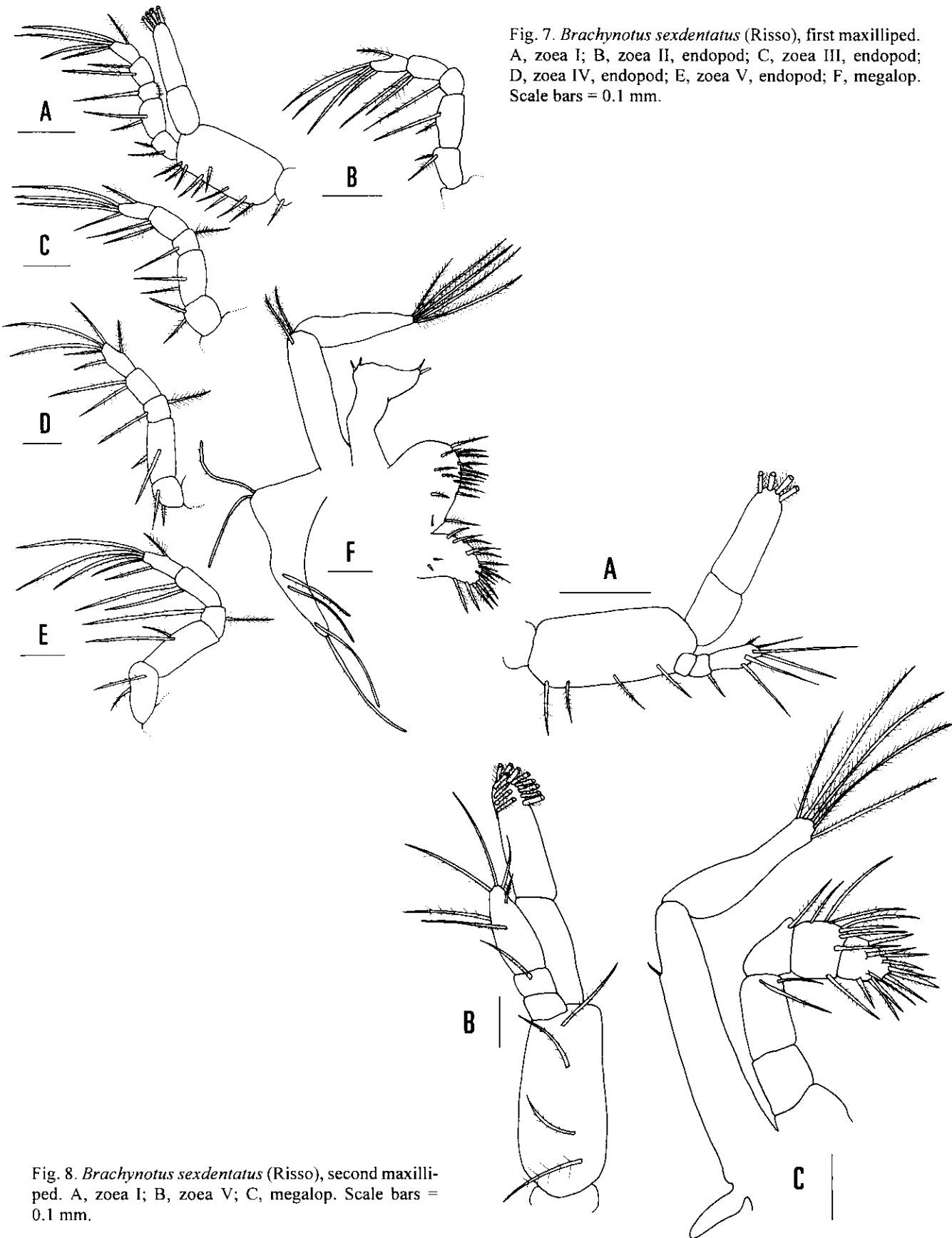


Fig. 7. *Brachynotus sexdentatus* (Risso), first maxilliped. A, zoea I; B, zoea II, endopod; C, zoea III, endopod; D, zoea IV, endopod; E, zoea V, endopod; F, megalop. Scale bars = 0.1 mm.

Fig. 8. *Brachynotus sexdentatus* (Risso), second maxilliped. A, zoea I; B, zoea V; C, megalop. Scale bars = 0.1 mm.

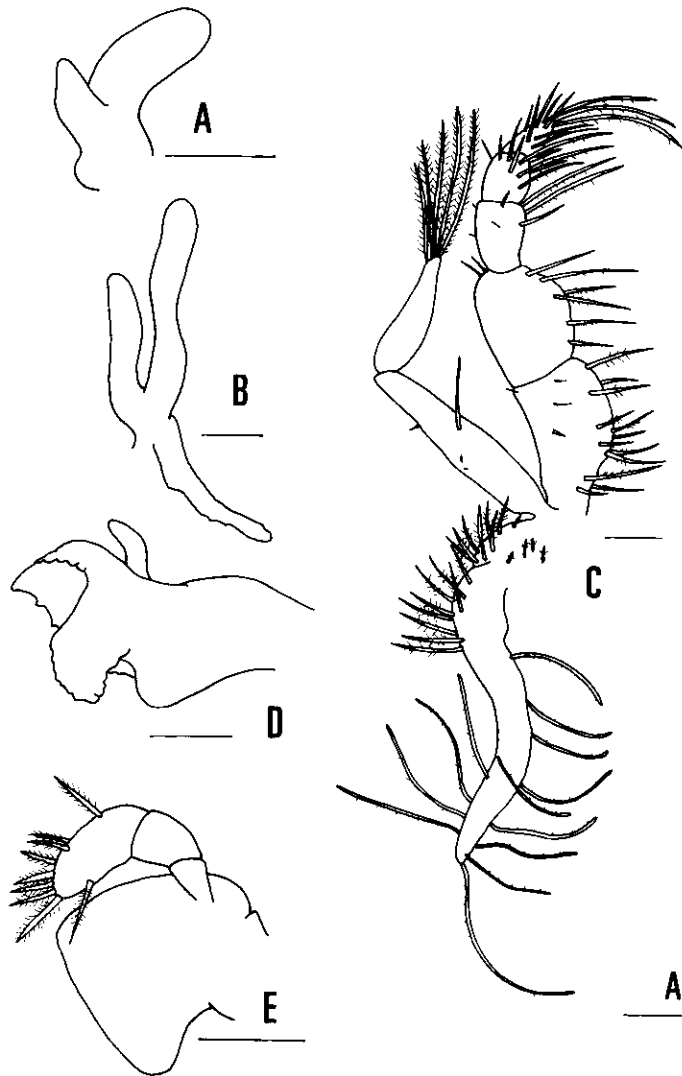


Fig. 9. *Brachynotus sexdentatus* (Risso), third maxilliped. A, zoea IV; B, zoea V; C, megalop. Mandible, D, zoea V; E, megalop. Scale bars = 0.1 mm.

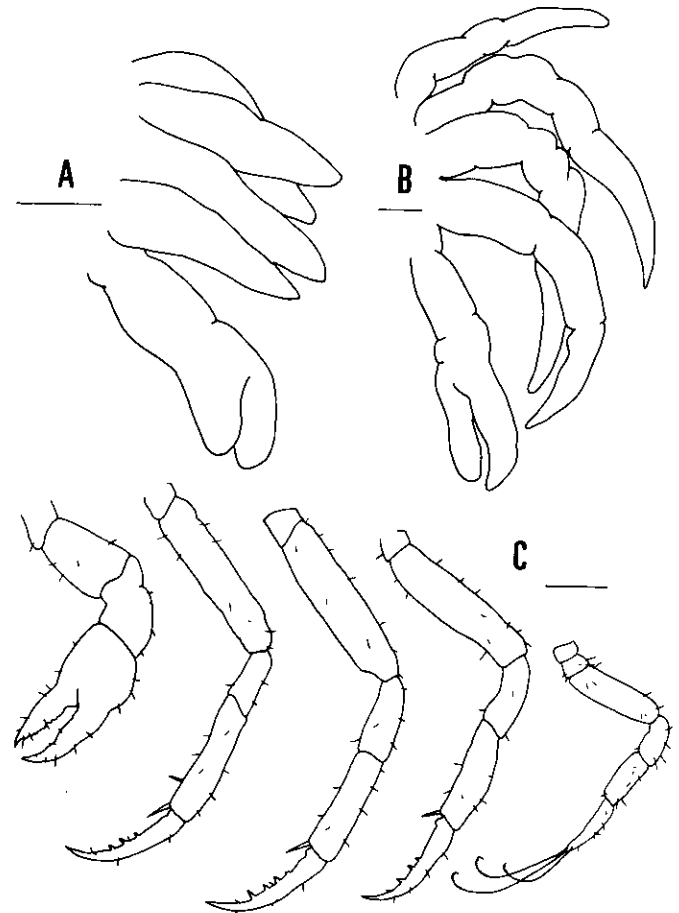


Fig. 10. *Brachynotus sexdentatus* (Risso), pereopod. A, zoea IV; B, zoea V; C, megalop. Scale bars, A,B = 0.1 mm, C= 0.3 mm.



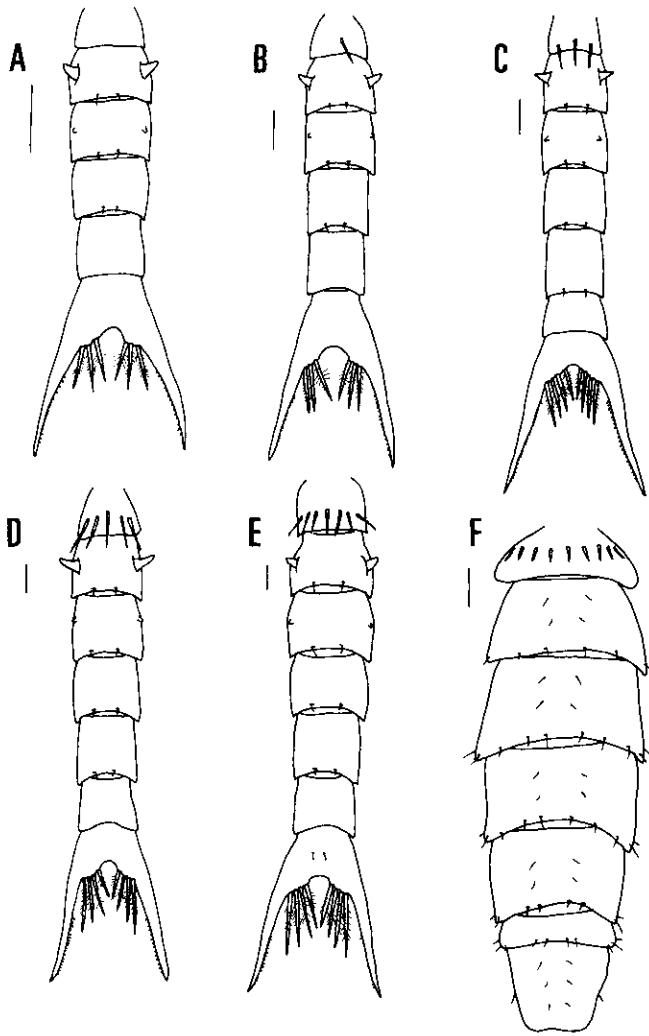


Fig. 11. *Brachynotus sexdentatus* (Risso), abdomen, dorsal view. A, zoea I; B, zoea II; C, zoea III; D, zoea IV; E, zoea V; F, megalop. Scale bars = 0.1 mm.

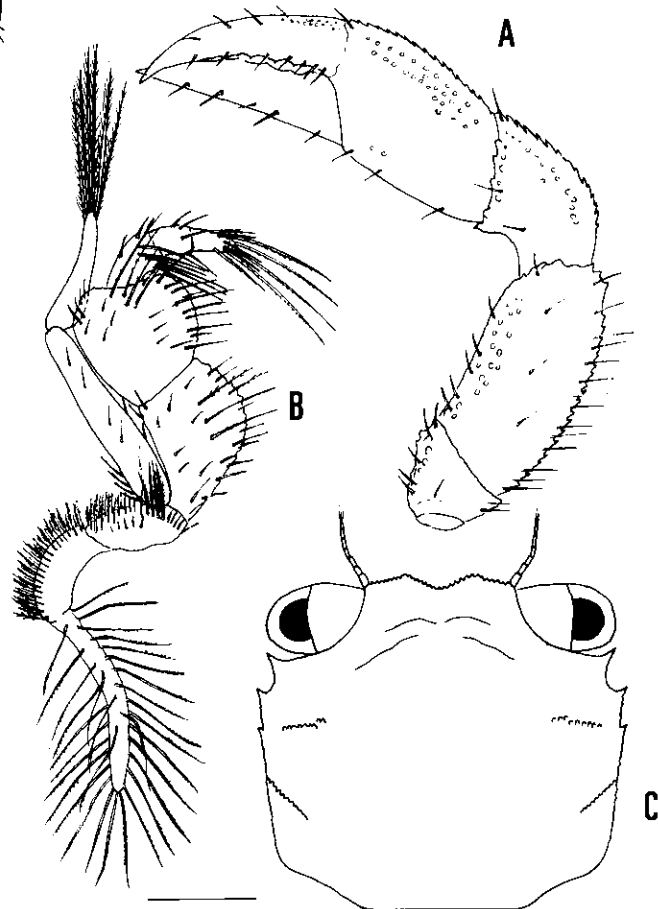


Fig. 12. *Brachynotus sexdentatus* (Risso), first crab. A, cheliped; B, third maxilliped; C, dorsal view of cephalothorax. Scale bar, A,B = 0.5 mm, C = 0.25 mm.

**Zoea III**

*Carapace* (Fig. 1C). Dorsal spine with 2 pairs of simple setae. Two pairs of anterodorsal setae. Each ventral margin with 7 plumodenticulate setae. Otherwise unchanged.

*Antennule* (Fig. 3C). Unchanged.

*Antenna* (Fig. 4C). Endopod bud present. Otherwise unchanged.

*Mandible*. Unchanged.

*Maxillule* (Fig. 5C). Unchanged.

*Maxilla* (Fig. 6C). Scaphognathite with 13 plumose marginal setae. Otherwise unchanged.

*First maxilliped* (Fig. 7C). Endopod 3rd segment with one additional dorsal plumose seta. Exopod distal segment with 8 natatory setae. Otherwise unchanged.

*Second maxilliped*. Exopod distal segment with 8 natatory setae. Otherwise unchanged.

*Third maxilliped*. Present as undifferentiated bud.

*Pereiopods*. Present as rudimentary buds.

*Abdomen* (Fig. 11C). Six abdominal somites. First somite with 3 long mid-dorsal setae. Now, 1 pair of posterodorsal setae on fifth somite. Somite sixth without setae. Otherwise unchanged.

*Telson* (Fig. 11C). Posterior margin now with 4 pairs of serrulate setae. Otherwise unchanged.

**Zoea IV**

*Carapace* (Fig. 1D). Dorsal spine with 4 pairs of simple setae. Three pairs of anterodorsal setae. Posterior margin with 4 long plumodenticulate setae. Each ventral margin with 10 plumodenticulate setae. Otherwise unchanged.

*Antennule* (Fig. 3D). Now with one subterminal aesthetasc. Otherwise unchanged.

*Antenna* (Fig. 4D). Endopod longer, more than 1/2 of protopod length. Otherwise unchanged.

*Mandible*. Unchanged.

*Maxillule* (Fig. 5D). Coxal endite with 6 plumodenticulate setae. Basal endite with 12 setae (2 plumodenticulate cuspidate and 10 plumodenticulate). Epipod setae present. Otherwise unchanged.

*Maxilla* (Fig. 6D). Basal endite bilobed with 6+5 plumodenticulate setae. Scaphognathite with 18 plumose marginal setae. Otherwise unchanged.

*First maxilliped* (Fig. 7D). Distal segment of the endopod with one additional seta (now 2 subterminal + 4 terminal) setae. Exopod distal segment with 10 natatory setae. Otherwise unchanged.

*Second maxilliped*. Exopod distal segment with 10 natatory setae. Otherwise unchanged.

*Third maxilliped* (Fig. 9A). Biramous and unsegmented. Endopod longer than exopod.

*Pereiopods* (Fig. 10A). Present, unsegmented. Chelipeds bilobed.

*Abdomen* (Fig. 11D). First somite with 5 long mid-dorsal setae. Pleopod buds present on somites 2–5, endopod absent. Otherwise unchanged.

*Telson* (Fig. 11D). Unchanged.

**Zoea V**

*Carapace* (Fig. 1E). Dorsal spine with 5 pairs of setae. Four pairs of anterodorsal setae. Posterior margin with 5 long plumodenticulate setae. Each ventral margin with 15 plumodenticulate setae. Otherwise unchanged.

*Antennule* (Fig. 3E). Biramous. Endopod bud present. Exopod with 4 subterminal and 5 terminal aesthetascs and 1 terminal simple seta.

*Antenna* (Fig. 4E). Endopod elongated, same length than protopod. Otherwise unchanged.

*Mandible* (Fig. 9D). Unsegmented palp present.

*Maxillule* (Fig. 5E). Coxal endite with 8 plumodenticulate setae. Basal endite with 16 setae (2 plumodenticulate cuspidate and 14 plumodenticulate). Otherwise unchanged.

*Maxilla* (Fig. 6E). Coxal endite bilobed with 3+8 plumodenticulate setae. Basal endite bilobed with 8+7 plumodenticulate setae. Scaphognathite with 29 plumose marginal setae. Otherwise unchanged.

*First maxilliped* (Fig. 7E). Exopod distal segment with 12 natatory setae. Otherwise unchanged.

*Second maxilliped* (Fig. 8B). Exopod distal segment with 12 natatory setae. Otherwise unchanged.

*Third maxilliped* (Fig. 9B). Endopod and exopod more elongated. Epipodite present.

*Pereiopods* (Fig. 10B). Chelipeds and pereiopods slightly segmented.

*Abdomen* (Fig. 11E). First somite with 7 long mid-dorsal setae. Pleopods elongated, endopod bud present. Otherwise unchanged.

*Telson* (Fig. 11E). One pair of dorsomedial simple setae on the telson plate. Otherwise unchanged.

**Megalop**

*Carapace* (Fig. 2A). Longer than broad. Rostrum ventrally deflected (approximately 90°) with a medium cleft. Setal arrangement as figured.

*Antennule* (Fig. 3F). Peduncle 3-segmented with 6, 3, 1 setae, respectively. Endopod unsegmented with 1 subterminal and 2 terminal setae. Exopod 4-segmented with 0, 6, 6 and 4 aesthetascs respectively and 0, 0, 1, 2 (1 simple, 1 long plumose) setae respectively.

**Antenna** (Fig. 4F). Peduncle 3-segmented with 2, 2, 1 setae, respectively. Flagellum 7-segmented with 0, 0, 4, 1, 5, 3, 3 (terminal) setae respectively.

**Mandible** (Fig. 9E). Palp 3-segmented with 9 (1 subterminal, 8 terminal) setae on distal segment.

**Maxillule** (Fig. 5F). Coxal endite with 15 marginal and 3 inner plumodenticulate setae. Basial endite with 23 marginal and 2 inner plumodenticulate setae. Endopod 2-segmented, proximal segment with 2 setae, and distal segment with 4 setae. Otherwise unchanged.

**Maxilla** (Fig. 6F). Coxal endite bilobed with 5 + 15 plumodenticulate setae. Basial endite bilobed with 11 (2 inner) + 16 (3 inner) plumodenticulate setae. Endopod unsegmented and without setae. Scaphognathite with 46 plumose marginal setae and 5 (3+2) lateral setae.

**First maxilliped** (Fig. 7F). Epipod with 6 long setae. Coxal endite with 17 plumodenticulate setae (2 inner). Basial endite with 17 plumodenticulate setae (5 inner). Endopod unsegmented with 4 simple setae. Exopod 2-segmented, proximal segment with two distal plumodenticulate setae, distal segment with 5 long terminal plumose feeding setae.

**Second maxilliped** (Fig. 8C). Epipodite slightly elongated and without setae. Coxa and basis not differentiated and without setae. Endopod 5-segmented, ischium unarmed, merus, carpus, propodus and dactylus with 2, 1, 8 and 11 plumodenticulate setae, respectively. Exopod 2-segmented, proximal with one medial seta and distal segment with 5 long terminal plumose feeding setae.

**Third maxilliped** (Fig. 9C). Epipod elongated with 9 plumodenticulate setae on the proximal part and 13 processes on distal one. Coxa and basis not differentiated with 12 plumodenticulate setae. Endopod 5-segmented, ischium, merus, carpus, propodus and dactylus with 16, 8, 7, 9 and 10 plumodenticulate setae, respectively. Exopod 2-segmented, proximal segment with 2 medial setae and 2 minute basal setae, and distal segment with 5 long terminal plumose raptatory setae.

**Pereiopods** (Fig. 10C). All segments well differentiated and with setae as figured. Propodus of pereiopods 2–4 with a long terminal inner spine. Dactylus of pereiopod 2–4 with 3 strong spines. Dactylus of fifth pereiopod with three long subterminal setae.

**Abdomen** (Fig. 11F). Six somites present. Somite 1 with 3 pairs of lateral setae and 9 mid-dorsal simple setae. Somite 2 with 1 pair of posterolateral setae, 2 pairs of mid-dorsal setae. Somites 3–5 with 2 pairs of posterolateral setae and 2 pairs of mid-dorsal setae. Somites 3–4 with 3 pairs of posterodorsal setae. Somite

5–6 with 2 pairs of posterodorsal setae. Somite 6 with 3 posterolateral setae. Somites 2–5 with one pair of biramous pleopods, endopod unsegmented with 3 terminal hooked setae, exopod unsegmented (Fig. 2B), pleopods 1–4 with 15, 16, 18, 16 long marginal plumose natatory setae, respectively. Uropods 2-segmented on somite 6, proximal segment with 1 long marginal plumose natatory seta and distal segment with 9 long marginal plumose natatory setae (Fig. 2C).

**Telson** (Fig. 11F,G). Squared in shape, with 6 mid-dorsal setae, and 1 pair of lateromarginal setae.

### First crab

**Carapace** (Fig. 11C), slightly broader than long, with 3 acute protrusions (anterolateral teeth) on the anterolateral margin; frontal margin rounded, denticulated, with a medial dip; posterolateral margin rounded. Chelipeds (Fig. 11A) stout, equal in size, setation as illustrated; pereiopods subequal with margin slightly denticulated. Third maxilliped (Fig. 11B), epipod elongated with 32–34 plumodenticulate setae on the proximal part and 31–32 processes on distal one. Coxa and basis not differentiated with 28–29 plumodenticulate setae. Endopod 5-segmented, ischium, merus, carpus, propodus and dactylus with 23, 27, 9, 4 and 9 plumodenticulate setae, respectively. Exopod 2-segmented, proximal segment with 5 medial setae and 4 basal setae, and distal segment with 6 long terminal plumose raptatory setae.

### Discussion

The morphology of the zoeal and megalopal stages of *Brachynotus sexdentatus* as described in this study includes all the features that are diagnostic for the Varunidae (see below). A comparison with the descriptions of plankton-collected *B. sexdentatus* (zoea I, III–V and megalop) by Bourdillon-Casanova (1960) is difficult since her brief descriptions do not include many details about the setation of the appendages. However, the few comparable characters are identical to those described in this study. Paula (1987) also attributed two zoeae from the plankton to *B. sexdentatus*. The first one, a zoea II, closely corresponds to the zoea II from this study. It only differs in size (rdl: 2.11 mm vs. 1.71 mm), but size differences are frequent between planktonic and cultured larvae. The other zoea (S5) described by Paula (1987) is similar to the final zoeal stage of *B. sexdentatus*. The only difference is the setation of the first maxilliped endopod. Paula (1987) reported 2,3,2,2,6, while in this

study and other descriptions (see Rodríguez et al., 1992; Guerao et al., 1995), the setation is recorded as 2,2,2,2,6. The additional seta observed by Paula (1987) is acquired in the third zoeal stage of many other genera and species of Varunidae and Sesarmidae, but not in *Brachynotus*. Also, the differences in size are more prominent (rdl: 5.4 mm vs. 3.35 mm). Based on these differences, we cannot confirm with certainty whether Paula's (1987) S5-larva represents a fifth zoeal stage of *B. sexdentatus*.

When compared to the early stages of congeneric species, *B. sexdentatus* (and *B. gemmellari*) can be easily distinguished from *B. atlanticus* by the presence of dorsolateral processes on the abdominal somite 3, which are absent in *B. atlanticus*. However, *B. sexdentatus* zoeas and megalops are very similar to those of *B. gemmellari*, and only minor differences can be observed in the setation of appendages (Table 2). There were also no significant differences in morphometric comparisons. The degree of variability in setation found between these species can often be found between larvae of the same genus or even species (Spivak and Cuesta, 2000). The larval differences found between *B. sexdentatus* and *B. gemmellari* are therefore currently insufficient for species separation based on larval morphology. Many more hatches of both species need to be compared in order to determine how consistent these differences are and if they can be used as diagnostic characters. The question raised by mtDNA studies, whether *B. sexdentatus* and *B. gemmellari* represent different ecophenotypes of the same species or whether they are the result of a very recent speciation event (Schubart et al., in press) cannot therefore be answered in this study. But, larval characters (e.g., differences in abdominal dorsolateral processes) appear to confirm that the two species represent sister species when compared to *Brachynotus atlanticus* and other species of Varunidae. Although larvae of *Brachynotus foresti* remain undescribed, according to the phylogeny and speciation model presented by Schubart et al. (in press), this species would be expected to be morphologically closer to *B. atlanticus*.

At the intergeneric level, there are only minor differences in setation between the Atlantic genera *Brachynotus* and *Cyrtograpsus* (see Spivak and Cuesta, 2000). These two genera can be distinguished from the rest of Varunidae by the morphology of the telson, which only acquires one pair of serrulate setae on the posterior margin in the course of the development. In contrast, the rest of Varunidae acquire two or three pairs of serrulate setae. DNA analysis of

the 16S rRNA, however, suggests a closer relationship between *Cyrtograpsus* and *Chasmagnathus* than with *Brachynotus* (Schubart et al., in press)

At present, there are larval data for less than 60% of the varunid genera (35% of the species). Several morphological characters of the known larvae are consistent within Varunidae and allow this taxon to be separated from the rest of grapsoid families (see Tables 3 and 4).

There are characters that are common in early stages of Varunidae, but their expression is not consistent in all genera or species. For example, the dorsal and rostral spines of the zoeal cephalothorax are normally long and straight, and lateral spines are well developed. However, there are known exceptions: *Acmaeopleura parvula*, *Gaetice depressus*, *Helice leachi* and *Cyctograpsus intermedius*. In the megalops, the pleopods have three terminal hooked setae on the endopod, except *Acmaeopleura parvula* which has two and *Varuna litterata* with four. A combination of several larval characters has also been found to be diagnostic for other grapsoid families, the Grapsidae *s. str.* (see Cuesta and Schubart, 1999), Plagusidae and Sesarmidae (see Cuesta, 1999).

Setation of basis of first maxilliped (2,2,3,3), and setation of endopod of the second maxilliped (0,1,6) of Varunidae are shared with members of the family Sesarmidae. Other characters, like the setation of the endopod of the maxilla (2,2), are shared with Grapsidae *s. str.* The larval morphology of Varunidae also shows close affinity to the one of Gecarcinidae. Zoeas of varunids differ from *Gecarcinus* and *Gecarcoidea* only in the setation of the endopod of second maxilliped (1,1,6), and from *Cardisoma* and *Epigrapsus* in this same setation pattern plus the setation of the maxillar endopod (2,3). In the case of the megalops, the main difference is the absence of the epipodite of the second maxilliped in the Gecarcinidae.

The absence of apomorphic characters in varunid early stages, as well as its close relationship to Gecarcinidae within the Grapsoidea, and the Macro-phthalminae within the Ocypodidae (see Cuesta, 1999) suggest a basal position of this family within the superfamily Grapsoidea. A basal position of *Varuna* within the Thoracotremata has previously been suggested by Jamieson et al. (1996) based on sperm morphology. Additional comparative studies of sperm, larval, and adult morphology as well as of various molecular markers will be needed to determine with certainty the exact phylogenetic position of the Varunidae within the Brachyura Thoracotremata.

Table 2. Morphological differences between zoeal and megalopal stages of *Brachynotus gemmellari*, *B. atlanticus* and *B. sexdentatus*

|                     | <i>B.<br/>gemmellari</i><br>Guerao et al.<br>(1995) | <i>B.<br/>sexdentatus</i><br>Present<br>study | <i>B.<br/>atlanticus</i><br>Rodríguez<br>et al.<br>(1992) |
|---------------------|---|---|---|
| <b>ZOEA I</b>       |   |   |   |
| <b>Antennule</b>    |   |   |   |
| a, s                | 2, 1  | 3, 1  | 2, 1  |
| <b>Abdomen</b>      |   |   |   |
| 2nd somite dlp      | present   | present                                       | present   |
| 3rd somite dlp      | present   | present                                       | absent  |
| <b>ZOEA II</b>      |   |   |   |
| <b>Carapace</b>     |   |   |   |
| Dorsal spine s.     | 0   | 1   | 0   |
| Posterior margin s. | 0   | 1   | 1   |
| Ventral margin s.   | 0   | 1   | 1   |
| <b>Antennule</b>    |   |   |   |
| a, s                | 3, 1  | 4, 1  | 4, 1  |
| <b>Maxilla</b>      |   |   |   |
| Coxal endite s.     | 3+3   | 3+5   | 3+3   |
| <b>Abdomen</b>      |   |   |   |
| 2nd somite dlp      | present   | present                                       | present   |
| 3rd somite dlp      | present   | present                                       | absent  |
| <b>ZOEA III</b>     |   |   |   |
| <b>Carapace</b>     |   |   |   |
| Ventral margin s.   | 6   | 7   | 5   |
| <b>Antennule</b>    |   |   |   |
| a, s.               | 3, 1  | 4, 1  | 4, 1  |
| <b>Maxillule</b>    |   |   |   |
| Basial endite s.    | 8   | 7   | 8   |
| <b>Maxilla</b>      |   |   |   |
| Coxal endite s.     | 3+3   | 3+5   | 3+4   |
| Scaphognatite s.    | 12  | 13  | 14  |
| <b>Abdomen</b>      |   |   |   |
| 2nd somite dlp      | present   | present                                       | present   |
| 3rd somite dlp      | present   | present                                       | absent  |
| <b>ZOEA IV</b>      |   |   |   |
| <b>Carapace</b>     |   |   |   |
| Dorsal spine s.     | 3   | 4   | 5   |
| Anterodorsal s.     | 2   | 3   | 2   |
| Posterior margin s. | 3   | 4   | 3   |
| Ventral margin s.   | 9   | 10  | 13  |
| <b>Antennule</b>    |   |   |   |
| a, s.               | 4, 1  | 5, 1  | 5, 1  |
| <b>Maxillule</b>    |   |   |   |
| Coxal endite s.     | 7   | 6   | 8   |
| Basial endite s.    | 10  | 12  | 12  |
| <b>Maxilla</b>      |   |   |   |
| Coxal endite s.     | 3+4   | 3+5   | 3+5   |
| Basial endite s.    | 6+5   | 6+5   | 6+6   |
| Scaphognatite s.    | 16  | 18  | 25  |
| <b>Abdomen</b>      |   |   |   |
| 2nd somite dlp      | present   | present                                       | present   |
| 3rd somite dlp      | present   | present                                       | absent  |

|                          | <i>B.<br/>gemmellari</i> | <i>B.<br/>sexdentatus</i> | <i>B.<br/>atlanticus</i> |
|--------------------------|--------------------------|---------------------------|--------------------------|
| <b>ZOEA V</b>            |                          |                           |                          |
| <b>Carapace</b>          |                          |                           |                          |
| Dorsal spine s.          | 5                        | 5                         | 6                        |
| Anterodorsal s.          | 3                        | 4                         | 3                        |
| Posterior margin s.      | 6                        | 8                         | 5                        |
| Ventral margin s.        | 14                       | 15                        | 17                       |
| <b>Antennule</b>         |                          |                           |                          |
| a, s.                    | 6, 1                     | 9, 1                      | 8, 1                     |
| <b>Maxillule</b>         |                          |                           |                          |
| Coxal endite s.          | 9                        | 8                         | 7                        |
| Basial endite s.         | 13                       | 16                        | 16                       |
| <b>Maxilla</b>           |                          |                           |                          |
| Coxal endite s.          | 3+7                      | 3+8                       | 3+10                     |
| Basial endite s.         | 8+7                      | 8+7                       | 9+6                      |
| Scaphognatite s.         | 25                       | 29                        | 29                       |
| <b>Abdomen</b>           |                          |                           |                          |
| 2nd somite dlp           | present                  | present                   | present                  |
| 3rd somite dlp           | present                  | present                   | absent                   |
| <b>MEGALOP</b>           |                          |                           |                          |
| <b>Antennule</b>         |                          |                           |                          |
| Peduncle s.              | 6, 4, 1                  | 6, 3, 1                   | 2, 4, 1                  |
| Endopod s.               | 3                        | 3                         | 4                        |
| Exopod (a) (s.)          | (6, 6, 5) (0, 2, 2)      | (0, 7, 6, 4) (0, 0, 1, 2) | (6, 6, 4) (0, 2, 1)      |
| <b>Antenna</b>           |                          |                           |                          |
| Peduncle s.              | 3, 2, 2                  | 2, 2, 1                   | 2, 2, 0                  |
| Endopod s.               | 0, 0, 4, 2, 4, 3, 3      | 0, 0, 4, 1, 5, 2, 3       | 0, 0, 4, 2, 5, 3, 3      |
| <b>Mandible palp</b>     |                          |                           |                          |
|                          | 0, 0, 7                  | 0, 0, 9                   | 0, 0, 8                  |
| <b>Maxillule</b>         |                          |                           |                          |
| Coxal endite s           | 19                       | 18                        | 22                       |
| Basial endite s          | 24                       | 25                        | 23                       |
| <b>Maxilla</b>           |                          |                           |                          |
| Coxal endite s.          | 5+13                     | 5+15                      | 5+16                     |
| Basial endite s.         | 8+10                     | 11+16                     | 8+12                     |
| Scaphognatite            | 49                       | 52                        | 47                       |
| <b>First maxilliped</b>  |                          |                           |                          |
| Coxal endite s.          | 10                       | 17                        | 19                       |
| Basial endite s.         | 8                        | 17                        | 8                        |
| Endopod s.               | 3                        | 4                         | 2                        |
| Exopod s.                | 2, 4                     | 2, 6                      | 3, 4                     |
| Epipodite s.             | 6                        | 6                         | 7                        |
| <b>Second maxilliped</b> |                          |                           |                          |
| Endopod                  | 0, 1, 1, 5, 8            | 0, 1, 1, 6, 9             | 0, 1, 1, 9, 9            |
| <b>Third maxilliped</b>  |                          |                           |                          |
| Endopod s.               | 15, 8, 4, 9, 9           | 16, 8, 7, 9, 10           | 14, 9, 7, 10, 8          |
| Exopod s.                | 2, 5                     | 4, 5                      | 1, 5                     |
| Epipodite s.             | 11+7                     | 11+13                     | 11+19                    |
| <b>Abdomen</b>           |                          |                           |                          |
| Pleopods s.              | 13-17                    | 15-18                     | 16-19                    |

s, setation (in carapace, setation refer to pairs of setae); a, aesthetascs; dlp, dorsolateral processes.

Table 3. Zoal characters of Varunidae

|  |  |
|--|--|
| Antenna                                    | Well developed exopod (>1/4 of the protopod length) and with 1 or 2 medial setae   |
| Maxilla, endopod setation                  | 2, 2   |
| First maxilliped, basis setation           | 2, 2, 3, 3   |
| Second maxilliped, endopod setation        | 0, 1, 6  |
| Abdomen, dorsolateral processes on somites | 2, 2-3 or 2-4, but never 2-5.  |
| Telson                                     | Simple, without lateral spines. Length of furcal arms longer than base of telson. Number of pairs of serrulate setae at the posterior margin increases through development (acquiring from 1 to 4 pairs) |

Table 4. Megalopal characters of Varunidae

|  |  |
|--|--|
| Antenna, flagellum segments              | 7  |
| Maxilla, lateral setae on scaphognathite | 3 anterior, 2 posterior  |
| Pereiopods 2-5, dactyli                  | Without denticulation on inner surface, in some cases only strongly spinulated |
| Uropod, distal segment setation          | 8-19   |

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## APPENDIX

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