JOURNAL OF NATURAL HISTORY, 1989, **23**, 205–217

Zoeal development of *Ethusa microphthalma* Smith, 1881 (Brachyura, Dorippidae) reared in the laboratory, with a comparison of other dorippid zoeae

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(*Accepted 23 June 1988*)

The complete zoeal development of a dorippid crab in the subfamily Ethusinae is described for the first time from a known parental female. The ovigerous *Ethusa microphthalma* was collected in the northern Gulf of Mexico off Louisiana. Larvae passed through four zoeal stages, and the megalopa was reached in 59 days at 20°C and 35 ppt salinity. The larvae differ from those of the few other dorippids for which a zoea is known. Salient distinguishing features include long lateral carapace spines, the presence of six setae on the endopod of the maxillule and maxilla, and a spinose antennal exopod lacking projecting mid-length spines or setae. Zoeal characters are compared to those known for the allied subfamily Dorippinae, and all references to zoeae of the Dorippidae are tabulated.

KEYWORDS: Brachyura, larvae, Dorippidae, Ethusinae, development, descriptions.

Introduction

Crabs of the family Dorippidae are small to large brachyurans typically found in deep waters of the continental shelf and upper continental slope. They have in the past been placed with the calappids and leucosiids in the section Oxystomata, although most workers acknowledge that this grouping is artificial (see Rice, 1980a). Larval evidence has been used to argue for separation of the constituent families (Rice, 1980a, b), but although complete larval development is known for at least one calappid and several leucosiids (see Rice, 1980b), few species of the Dorippidae, and no species of the subfamily Ethusinae, have ever been reared through all of the zoeal stages. Rice (1980b) reviewed and summarized descriptions of dorippid zoeae, all of which were from the plankton except for one account of the first zoeae of *Ethusa mascarone* (Herbst) hatched from eggs (Heegaard, 1963). Since Rice's review, the complete development of three species of the Dorippinae has been described (Terada, 1981), and additional reports exist for zoeal stages collected in plankton tows (Paula, 1987; Quintana, 1987). In the subfamily Ethusinae, larvae are known only for *Ethusa investigatoris* Alcock (Menon, 1937) and *E. mascarone* (Herbst) (see Cano, 1891; Williamson, 1915; Bourdillon-Casanova, 1960; Heegaard, 1963; Paula, 1987). However, Menon's (1937) description is almost certainly of a Dorippinae (and not Ethusinae) zoea, as the carapace lacks lateral spines (see Discussion). Most previous

0022-2933/89 $5·00

authors described only one zoeal stage, and the descriptions of others were limited to a series or partial series reconstructed from the plankton (see Table 2).

Ethusa microphthalma Smith is known from deep (83 to 752 m; rarely to 20 m) waters from Martha's Vineyard, Massachusetts, to west Florida and Cuba and around the Gulf of Mexico (Rathbun, 1937; Williams, 1984), and from 1830 m in the Azores (Miers, 1886: 329). Below we describe the four zoeal stages of *E. microphthalma* and comment on the significance of Ethusinae zoeal morphology.

Materials and methods

An ovigerous specimen of *E. microphthalma* was collected by a bottom trawl on October 19, 1982, at 28°42′N, 89°24′W (Gulf of Mexico, 22 km south of Southwest Pass, Mississippi River delta). Depth at the collection site was 115 m, and bottom water temperature was about 17°C. The specimen was held until hatching (November 3, 1982) in an insulated container of aerated and carbon-filtered seawater of 35 ppt salinity. Water temperature in the container was maintained at 16°–19°C by frequent addition of plastic bottles of frozen seawater. Vigorously swimming first-zoea larvae ($n = 45$) were placed in compartmentalized plastic trays, one larva per compartment. Each compartment contained about 25 ml of seawater (35 ppt salinity). Upon reaching the third zoea stage, each larva was moved to a separate glass finger bowl of 8 cm diameter containing approximately 60 ml seawater. Additional larvae were mass-cultured as follows: 10 first-zoea larvae in each of two glass finger bowls (10·5 cm diameter, 150 ml of seawater, 35 ppt salinity) and approximately 40 first-zoea larvae in a glass rectangular bowl (35 × 22·5 cm, 1200 ml seawater, 35 ppt salinity). Trays and bowls were placed in a constant-temperature chamber at 20°C and under a light regimen of 12 h L:12 h D. Each day seawater was changed in compartments and bowls, and larvae were fed freshly hatched brine-shrimp nauplii (Brazilian source).

Exuviae, dead larvae, and a developmental series of larvae from the mass cultures were preserved in 70% ethanol. Illustrations were made from dead larvae, and accuracy was checked by examination of molts. Drawings were made with the aid of a Wild M-11 compound microscope and camera lucida; accuracy was verified with a Nikon Optiphot. Abbreviations used in the descriptions are as follows: CL = carapace length (measured from the orbit to the posterior carapace border); RS = rostral spine; DS = dorsal carapace spine; LS = lateral carapace spine; AB = abdomen. Meristic values of setation are given in a proximal-to-distal direction.

The parental female is deposited in the Zoological Collection of the University of Southwestern Louisiana, Lafayette, Louisiana; duplicates of the zoeal stages are deposited in the U.S. National Museum of Natural History, Washington, D.C., catalogued USNM No. 234432.

Rearing results

Hatching lasted about eight hours. At the beginning of the period, prezoeae were seen on the bottom of the hatching container, and a few of these moulted to first zoeae and swam to the surface. By the end of hatching, first-zoea larvae covered the water surface and the sides of the hatching container just above the water line. The elongate carapace spines of the larvae caused them to stick to surfaces and to become entangled with one another. Larvae in mass culture were continually entangled and had to be gently separated with forceps. These larvae, as well as those raised singly, damaged the carapace spines and caudal furcae on the sides of the container. Also, larvae became

fouled by brine shrimp debris sticking to the long spinulose carapace spines and caudal furcae.

We could not determine whether all first-zoea larvae hatched as prezoeae, or just those observed at the beginning of the hatching period. Four zoeal stages were followed by a megalopa (Table 1). One fourth-zoea larva reached the megalopa stage 59 days after hatching, and two others died in moult to megalopa, 59 and 61 days after hatching. The megalopa specimen was lost before it could be described and illustrated.

Table 1. Duration (mean, standard error, range) and survival of larval stages of *Ethusa microphthalma* at 20°C and 35 ppt salinity reared singly in compartmental plastic trays ($n = 45$).

Stage	Duration (days)	Died in moult	Number moulting to next stage
First zoea	11·9 ± 0·17 (10–14)		34
Second zoea	10·3 ± 0·21 (9–14)		28
Third zoea	13·9 ± 0·51 (11–18)		19
Fourth zoea	23·7 ± 0·33 (23–24)	2	1
Megalopa			0

Descriptions of the zoeae

First zoea

Size: CL = 0·7 mm, RS = 2·4 mm, DS = 2·3 mm, LS = 1·7 mm, AB = 2·9 mm, tip of DS to tip of RS = 4·8 mm ($n = 10$).

Carapace (Fig. 1a, b): Smooth, more or less triangular, with well-developed lateral, dorsal, and rostral spines, each minutely spinulose on distal 2/3; posteroventral borders with few setae; small raised tubercle directly posterior to DS.

Antennule (Fig. 1c): Small, stout, conical, with 3–4 terminal aesthetascs.

Antenna (Fig. 1d): Protopod with paired, evenly spaced spines; area between spines armed with minute spinules increasing in size distally toward paired spine; exopod slightly longer than protopod, with evenly spaced spines mostly on medial border and with minute spinules on distal half.

Mandible: Not examined.

Maxillule (Fig. 1e): Endopod with 2 segments; proximal segment lacking setae; distal segment with 6 setae arranged 2+2+2; basal endite with 3–5 heavy spines and setae; coxal endite with 1 or 2 stout spines and 3–4 setae.

Maxilla (Fig. 1f): Endopod with 6 setae, arranged 1+2+3; basal endite bilobed with 4+4 setae; coxal endite bilobed with 3–4+3 setae; scaphognathite with 4 plumose setae spaced as illustrated and with plumose terminal process.

First maxilliped (Fig. 1g): Basis with 8–10 setae in groups of 2 or 3; endopod 5-segmented, setation 3–4, 2, 1, 2, 4; exopod indistinctly segmented, with 4 plumose natatory setae.

Second maxilliped (Fig. 1h, i): Basis with 2–3 setae; endopod 3-segmented, with setation 1, 1, and 4; seta of segment 2 and largest seta of segment 3 bearing stiff, evenly-spaced ventral spinules on proximal half and minute serrulations on distal half; exopod with 4 natatory setae.

Abdomen (Fig. 1j): All somites longer than wide; somite 2 with small dorsolateral knobs; somites 3–5 slender with small posteriorly directed spines but no setae on posterior border; somite 6 fused to telson.

Telson (Fig. 1k): Long and slender with stout, spinulose lateral spines at point halfway between indistinct margin of abdominal somite 6 and bifurcation of caudal furcae; caudal furcae spinulose, at least 3 times length of area proximal to bifurcation; medial indentation of furcae with 2 spinulose setae.

Second zoea

Size: CL = 1·0 mm, RS = 3·0 mm, DS = 1·7 mm, LS = 1·7 mm; AB = 3·1 mm, tip of DS to tip of RS = 5·0 mm ($n = 5$).

Carapace (Fig. 2a, b): As in first zoea but with slightly more setose posteroventral borders and with all carapace spines shorter relative to carapace length (although not quite as short as depicted in Fig. 2a, which was drawn at an angle slightly different from Figs. 1a, 3a, and 4a).

Antennule (Fig. 2c): With 5 or 6 aesthetascs and simple setae.

Antenna (Fig. 2d): Mostly unchanged, with paired spines and scattered spinules of protopod and exopod smaller relative to size of antenna; endopod not present.

Mandible: Not examined.

Maxillule (Fig. 2e): Unchanged except for slightly more spinose basal and coxal endites.

Maxilla (Fig. 2f): Endopod unchanged; basal and coxal endites with 4+4 and 3+3 setae, respectively; scaphognathite with 12–14 plumose setae.

First maxilliped (Fig. 2g): Basis unchanged; exopod with 6 natatory setae; endopod with 5 or 6 setae on distal segment.

Second maxilliped (Fig. 2h, i): Basis and endopod unchanged; exopod with 6 natatory setae.

Abdomen (Fig. 2j): As in first zoea but with single, long, pappose seta arising dorsally from somite 1 and with pair of small setae on posterior dorsal surface of somites 2–5; small spines of first zoea lacking; somite 6 remains fused to telson.

Telson (Fig. 2k): Lateral spines located almost equidistant from posterior border of somite 6 and tip of caudal furcae; caudal furcae shorter relative to telson length, equal to or shorter than area of telson proximal to bifurcation; small spinules now above lateral spines.

Third zoea

Size: CL = 1·6 mm, RS = 4·8 mm, DS = 4·0 mm, LS = 4·6 mm, AB = 5·2 mm, tip of DS to tip of RS = 5·3 mm ($n = 3$).

Carapace (Fig. 3a, b): As in previous stages but with more setose posteroventral borders.

Antennule (Fig. 3c): With 5–7 aesthetascs and setae, not arranged in tiers; no indication of endopod at this stage.

Antenna (Fig. 3d): Endopod now present as small protrusion approximately 1/7 length of exopod; protopod and exopod armed as in earlier stages.

Mandible: Not examined.

Maxillule (Fig. 3e): Endopod unchanged; basal and coxal endites both with 4–6 spines and 5–7 setae.

Maxilla (Fig. 3f): Endopod unchanged; basal endite with 4+5 setae; coxal endite with 4+5 setae; scaphognathite with 30–33 plummose setae.

FIG. 1. First zoea of *Ethusa microphthalma* Smith. a, lateral view; b, anterodorsal view, spines and abdomen omitted; c, antennule; d, antenna; e, maxillule; f, maxilla; g, first maxilliped; h, second maxilliped; i, endopod of second maxilliped; j, dorsal view of abdomen with somite 4 enlarged at right; k, telson and posterior border of abdominal somite 5, with distal 1/4 of caudal furca enlarged at right. Scale bars are labelled in millimetres.

FIG. 2. Second zoea of *E. microphthalma*. a, lateral view; b, frontal view, spines and abdomen omitted; c, antennule; d, antenna; e, maxillule; f, maxilla; g, first maxilliped; h, second maxilliped; i, endopod of second maxilliped; j, lateral view of abdomen; k, telson and posterior border of abdominal somite 6 (still fused). Scale bars are labelled in millimetres.

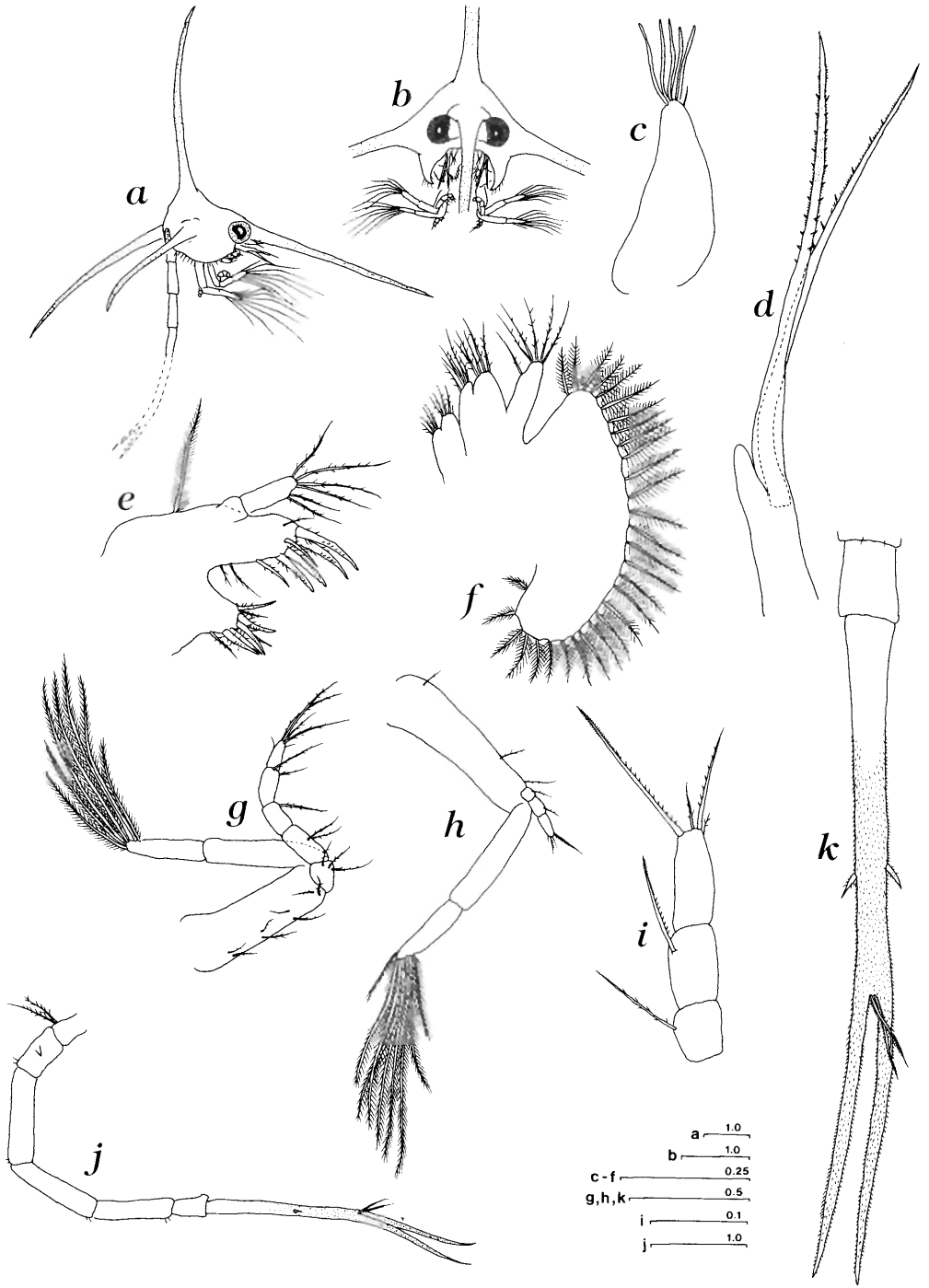

FIG. 3. Third zoea of *E. microphthalma*. a. lateral view; b, frontal view, spines and abdomen omitted; c, antennule; d, antenna; e, maxillule; f, maxilla; g, first maxilliped; h, second maxilliped; i, endopod of second maxilliped; j, lateral view of abdomen; k, telson, abdominal somite 6, and posterior border of abdominal somite 5. Scale bars are labelled in millimetres.

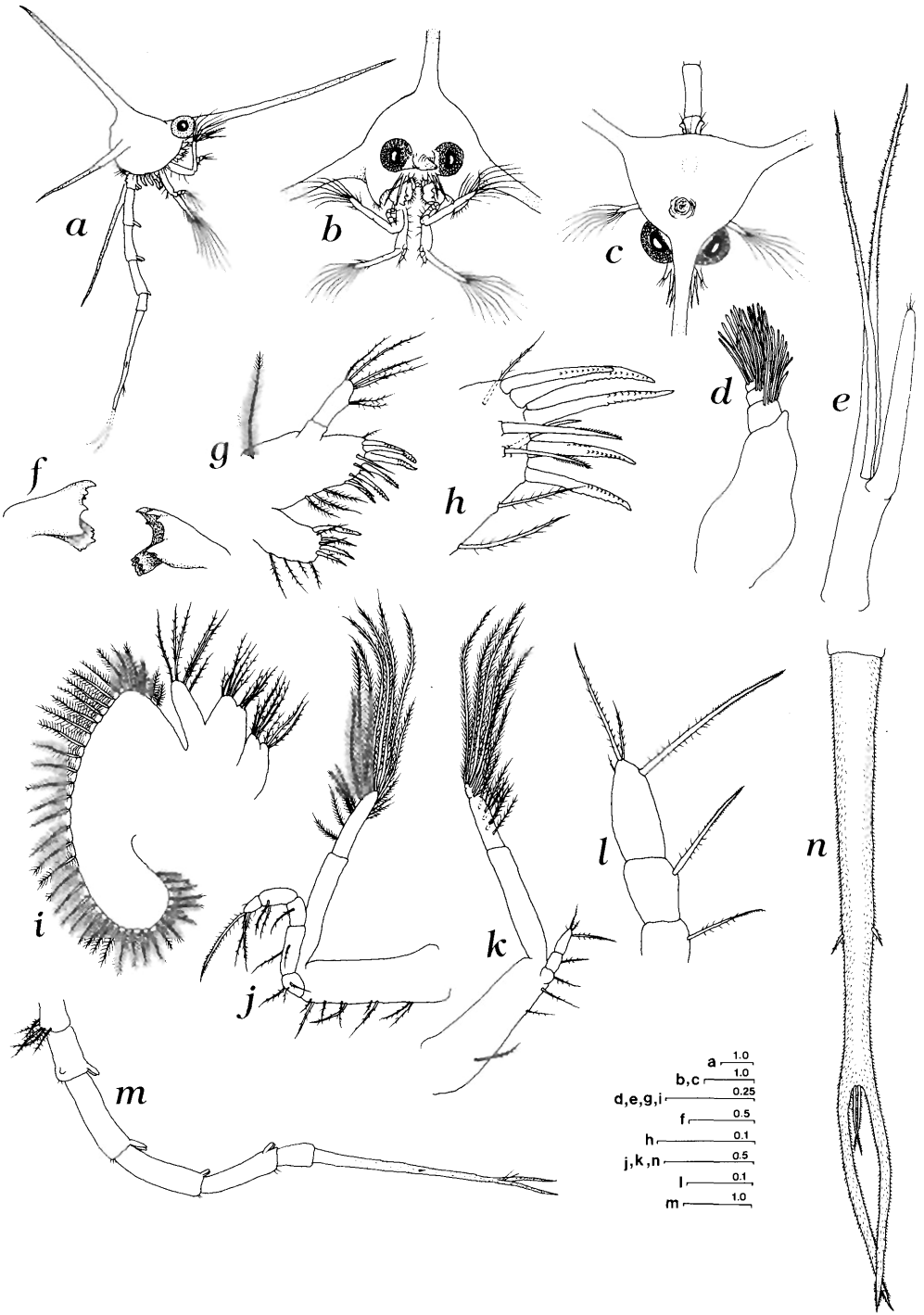

FIG. 4. Fourth zoea of *E. microphthalma*. a, lateral view; b, frontal view, spines and abdomen omitted; c, dorsal view; d, antennule; e, antenna; f, mandibles (outer view); g, maxillule; h, basal endite of maxillule; i, maxilla; j, first maxilliped; k, second maxilliped; l, endopod of second maxilliped; m, lateral view of abdomen; n, telson and posterior border of abdominal somite 6. Scale bars are labelled in millimetres.

First maxilliped (Fig. 3g): Basis unchanged; endopod with 6 setae on distal segment, 2 minute; exopod with 8–10 natatory setae.

Second maxilliped (Fig. 3h, i): Basis and endopod unchanged; exopod with 9–12 natatory setae.

Abdomen (Fig. 3j): As in second zoea but with 2 setae present on somite 1 and with somite 6 distinct from telson; pleopod buds not present.

Telson (Fig. 3k): Small spinules continuing well above (proximal to) stout lateral spines; length of furcae only about 2/3 length of telson proximal to bifurcation.

Fourth zoea

Size: CL = 2·1 mm, RS = 6·8 mm, DS = 5·6 mm, LS = 5·6 mm, AB = 7·4 mm, tip of DS to tip of RS = 8·7 mm (n = 3).

Carapace (Fig. 4a, b, c): Markedly triangular in lateral, frontal, and dorsal views; all carapace spines well-developed.

Antennule (Fig. 4d): With about 20 aesthetascs and setae arranged in 3 progressively smaller tiers; endopod present as small lateral bud.

Antenna (Fig. 4e): Endopod now about 1/2 length of protopod and exopod, with 2–3 small terminal setae.

Mandible (Fig. 4f): Large, well-developed; incisor process with four sharp teeth on 'outer' border and one small tooth on 'inner' border; molar process more or less oval and bearing numerous denticles.

Maxillule (Fig. 4g, h): Basal endite with 5–6 cuspidate spines and several setae as illustrated (Fig. 4h); coxal endite with 4–5 spines and 6–8 setae; endopod unchanged.

Maxilla (Fig. 4i): Endopod unchanged; basal endite with 5–6 + 5–6 setae; coxal endite with 4–5 + 3–4 setae; scaphognathite with 40–44 plumose setae.

First maxilliped (Fig. 4j): Basis and endopod as in third zoea; exopod with 15–18 natatory setae.

Second maxilliped (Fig. 4k, l): Basis and endopod unchanged; exopod with 13–17 natatory setae.

Abdomen (Fig. 4m): Somite 1 with 5 pappose setae on posterodorsal surface; somites 2–5 with small paired ventral pleopod buds; otherwise as in third zoea.

Telson (Fig. 4n): Entire telson armed with minute spinules; caudal furcae less than half length of area proximal to their bifurcation.

Discussion

Most early accounts of larval development in the Dorippidae (Table 2) do not contain sufficient information to allow detailed comparisons at the species level or higher. An additional problem is that some earlier works may include erroneous information. For example, the zoea described by Gilet (1952) as a '*metazoé*' and attributed to *Dorippe* (= *Medorippe*) *lanata* was supposedly held until it moulted to the megalopa stage, but Paula (1987), noting the absence of pleopods in Gilet's description, suspected that Gilet's description was of a stage 3 rather than a stage 4 zoea. It is possible that Gilet's illustration was not of the same individual that later moulted to the megalopa, as descriptions of the terminal (invariably the fourth) zoeal stage of other dorippids show small but distinct pleopods on abdominal somites 2 to 5. Bourdillon-Casanova (1960) also noted several discrepancies or inaccuracies in the descriptions of Cano (1891), Gilet (1952), and Kurian (1956), and the illustrations of Heegaard (1960) are not accurate (see Paula, 1987).

Aikawa (1933, 1937) described several zoeal stages of undetermined species of

Table 2. Descriptions of zoeal stages in the family Dorippidae MacLeay, 1838.

Subfamily Dorippinae		
Dorippe sp. A	zoea II	Aikawa, 1937
Dorippe sp. B	zoea IV	Aikawa, 1937
Dorippe frascone (Herbst)	zoea III, IV	Quintana, 1987
(as *Dorippe dorsipes* (Linnaeus))	zoea I–IV	Terada, 1981
Medorippe lanata (Linnaeus)	zoea I–IV§	Paula, 1987
(as *Dorippe lanata*)	zoea I	Boraschi, 1921
(as *Dorippe lanata*)	zoea I, II	Bourdillon-Casanova, 1960
(as *Dorippe lanata*)	zoea III or IV	Gilet, 1952
(as *Dorippe lanata*)	zoea I	Heegaard, 1963+
(as *Dorippe lanata*)	zoea I, II, IV	Cano, 1893
Nobilum japonicum japonicum (von Siebold)		
(as *Neodorippe japonica* (von Siebold))	zoea I–IV	Terada, 1981
Paradorippe granulata (de Haan)	zoea IV	Quintana, 1987
(as *Dorippe granulata*)	zoea I	Aikawa, 1937
(as *Dorippe granulata*)	zoea I–IV	Kurata, 1964
(as *Dorippe granulata*)	zoea I–IV	Terada,1981
Phyllodorippe armata Miers		
(as *Dorippe ?armata*) (ASM 12)	zoea I	Rice and Williamson, 1977
(as *Dorippe armata* White)	zoea I or II	Lebour, 1959
Uncertain Identification (probably *Dorippe*)		
(as "*Ethusozoea*" *koreana*)	zoea I	Aikawa, 1933
(as *Ethusa investigatorius* Alcock)	zoea I–IV	Menon, 1937
Subfamily Ethusinae		
Unidentified (as *Dorippe* sp.)	undetermined	Gurney, 1924¶
Ethusa mascarone (Herbst)	zoea I, II, IV	Cano, 1891++
	zoea I, II, IV	Kurian, 1956
	zoea I	Heegaard, 1963+
	zoea I–IV	Bourdillon-Casanova, 1960
	zoea I, III, IV	Paula, 1987
(as *Ethusa mascerone* Roux)	zoea I	Williamson, 1915¶
Ethusa microphthalma Smith	zoea I–IV	Present Study
"*Ethusozoea*" *lineata*	zoea I	Aikawa, 1933
Not *Ethusa investigatorius* Alcock as described by Menon (= *Dorippe*)		
Probable dorippids of unknown affinity		
"*Zoea clavata*" Leach	undetermined	see Gurney, 1942
?*Dorippe* sp.	undetermined	see Gurney, 1942
Unidentified (Z19)	zoea I, IV(?)	Andryszak, 1979

¶ Some characters repeated in table I of Aikawa, 1937.
§ Only characters omitted by Bourdillon-Casanova (1960) were described by Paula (1987).
+ Hatched from eggs; all other accounts, except Terada (1981), from planktonic material.
++ Not seen by us; information from Bourdillon-Casanova (1960).

Dorippe from the plankton and noted that they differed from larvae of *Ethusa* in that *Dorippe* larvae lack lateral carapace spines (Aikawa based his comparison with *Ethusa* on the description by Williamson, 1915, of larvae of *E. mascarone*, spelled *E. macerone* and *E. mascerone* by Aikawa, 1933, and *E. macerone* by Aikawa, 1937). Aikawa (1933, 1937) felt that dorippid larvae were collectively distinct enough to warrant a separate brachyuran zoeal grouping, named by him *Ethusozoea* and characterized by a "peculiar C-type" telson, naked basal segment of the endopod of the maxillule, and naked basal segment of the endopod of the second maxilliped. Rice (1980b), drawing

from a larger number of zoeal accounts, gave an expanded summary of dorippid larval characters. Salient distinguishing characters of dorippid larvae include: dorsal setae on abdominal somite 1; small lateral knobs on abdominal somite 2; pleopod buds not appearing until stage 4; long and spinulose telson with stout lateral spines proximal to level of bifurcation of the furcae; spinulose furcae with pairs of long spinulose setae arising from medial indentations; antennal exopod subequal in length to protopod and usually with two prominent spines at midlength; distal segment of endopod of maxillule with 3 or 4 setae; endopod of maxilla with single terminal group of 4 or 5 setae; scaphognathite with 3 or 4 setae in stage I; endopod of first maxilliped with 5 segments and setation 3, 2, 1, 2, 5; and endopod of second maxilliped with 3 segments and setation 0, 1, and 2 or 3. These characters appear to apply at least to the subfamily Dorippinae, although exceptions are known. For example, in the zoea tentatively identified as *Dorippe ? armata* (ASM 12, see Rice and Williamson, 1977), now known as *Phyllodorippe armata* (see Manning and Holthuis, 1981), the antennal exopod is only about half the length of the protopod, but Rice and Williamson note that it may have been broken in the single available specimen. Of the three species of the Dorippinae reared by Terada (1981), there is remarkable conformity with the characters given by Rice (1980b). The only difference seems to be that the spinulose setae of the telsonal indentation are very long, exceeding in length the relatively short caudal furcae. Quintana (1987) feels that the short caudal furcae are probably an abnormality, perhaps caused by laboratory rearing conditions. The detailed descriptions by Quintana (1987) of late zoeal stages of *Dorippe frascone* and *Paradorippe granulata* also agree with Rice's (1980b) summary of characters of dorippid zoeae. However, there are marked differences between zoeae of the subfamily Ethusinae, as described in the present study and in the redescription of *Ethusa mascarone* by Paula (1987), and those of the Dorippinae (see Terada, 1981). The most obvious difference is that known larvae in the Ethusinae have lateral carapace spines, which apparently are always absent in the Dorippinae. This difference may be of little phylogenetic importance, however, as lateral spines vary within several brachyuran families (see, e.g., Martin *et al.*, 1985). The Ethusinae antennal exopod lacks any midlength paired spines or setae like those seen in the Dorippinae; instead there is a series of unpaired spinules directed toward the spinose protopod. The endopod of the maxillule is more setose, with 6 setae arranged in groups of 2. The endopod of the maxilla is also more setose, with 6 setae either in two groups of 3 (Paula, 1987) or arranged 1 + 2 + 3 (present study). Finally, the 3-segmented endopod of the second maxilliped bears a single seta on the basal segment; this segment is always naked in the Dorippinae. The lateral carapace spines of *E. microphthalma* are much longer than those depicted for *E. mascarone* by Paula (1987), and the minute spinules on the rostral and dorsal carapace spines are not as obvious as those shown by Paula for *E. mascarone*. Otherwise, there are few differences between these two members of the Ethusinae.

Although the above differences between the larvae of *Ethusa* and the larvae of the Dorippinae necessitate a slight expansion of Rice's (1980b) characterization of the family Dorippidae, we do not believe the differences are of sufficient magnitude to bring into question the naturalness of the family. Other characters, such as the long and thin abdomen, long setae on the first abdominal somite, long and fairly simple telson with its unusually placed lateral spines, and few setae in the telsonal indentation, unite the two subfamilies and clearly distinguish them from all other brachyuran larvae. Rice (1980b) noted that it is "difficult to see a close relationship between them and the larvae of any other crab group", and unfortunately our observations on

development in *Ethusa microphthalma* do nothing more to bridge the gap.

Paula (1987) thought that the higher numbers of setae on appendages (maxillae, maxillipeds) in zoeae of *E. mascarone* and in the zoea called "*Ethusozeae*" *lineata* by Aikawa (1933), as compared to those on corresponding appendages in *Medorippe lanata*, might indicate a primitive condition in *Ethusa*. Paula (1987) therefore postulated that *Ethusa* (subfamily Ethusinae) may represent a link between ancestral dorippid larvae and those of the genus *Medorippe* (subfamily Dorippinae). The numbers of setae we report for the maxillae and maxillipeds of *E. microphthalma* are also greater than those on corresponding appendages of any zoeae of the Dorippinae. However, larval characters in the Decapoda may reflect adaptation to environment, and cases of apparent reversals in spinosity and setosity are known (see Williamson, 1982). For these reasons, we restrict our comments and say only that there appears to be sound evidence from the zoeal stages that the two dorippid subfamilies, Dorippinae and Ethusinae, are indeed separate lineages as recognized by Guinot (1977) on the basis of adult characters.

Acknowledgments

We thank the National Marine Fisheries Service, Southeast Fisheries Center, Pascagoula, Mississippi, for the opportunity to collect ovigerous crabs during Cruise 130 of the R/V *Oregon II*. We are grateful to Dr D. L. Felder for confirming the identification of the parental female and to Dr L. G. Abele for providing space and facilities for the descriptive stage of the study. Special thanks to Dr A. B. Thistle for editing and to C. G. Godfrey for typing early drafts. This work was supported in part by National Science Foundation grant no. BSR-8615018 to JWM and Lawrence G. Abele.

References

Aikawa, H., 1933. On larval forms of some Brachyura, paper II: a note on indeterminable zoeas. *Records of Oceanographic Works in Japan* **5**(2), 124–254.

Aikawa, H., 1937. Further notes on brachyuran larva. *Records of Oceanographic Works in Japan* **9**(1), 87–162.

Andryszak, B. L., 1979. Abundance, distribution, and partial descriptions of reptant decapod crustacean larvae collected from neritic Louisiana waters in July, 1976. M.S. thesis, Louisiana State University, Baton Rouge. 101 pages.

Boraschi, L., 1921. Osservazioni sulle larve die Crostacei Brachiuri e Anomuri. *R. Comitato Talassografico Italiano, Memoria* **87**, 1–32.

Bourdillon-Casanova, L., 1960. Le méroplancton du Golfe de Marseille; les larves de Crustacés Décapodes. *Recueil des Travaux de la Station Marine d'Endoume* **30**(18), 1–286.

Cano, G., 1891. Sviluppo postembrionale dei Dorippidei, Leucosiadi, Corystoidei e Grapsidi. *Memorie della Società Italiana di Scienze naturali* **8**(3), 1–4 [not seen; information from Bourdillon-Casanova, 1960].

Cano, G., 1893. *Dorippe*, studio morfologico. *Atti Accademia Scienze fisichee matematiche di Napoli* **6**(9), 1–9.

Gilet, R., 1952. Metazoé de *Dorippe lanata* (Linné) et sa mégalope. *Vie et Milieu* **3**(4), 415–420.

Guinot, D., 1977. Propositions pour une nouvelle classification des Crustacés Décapodes Brachyoures. *Comptes-rendus hebdomadaires des séances de l'Académie des Sciences* (Paris), series D, **285**, 1049–1052.

Gurney, R., 1924. Decapod larvae. *British Antarctic "Terra Nova" Expedition, 1910. Zoology, vol. 8, Crustacea, part 9: Decapod Larvae*: 37–202.

Gurney, R., 1942. *Larvae of decapod Crustacea*. Ray Society, London. 1–306.

Heegaard, P., 1963. Decapod larvae from the Gulf of Napoli hatched in captivity. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kjobenhaven* **125**, 449–493.

KURATA, H., 1964. Larvae of decapod Crustacea of Hokkaido. 8. Dorippidae (Brachyura). *Bulletin of the Hokkaido Regional Fisheries Research Laboratory* **29,** 71–74 (in Japanese with English summary).

KURIAN, C. V., 1956. Larvae of decapod Crustacea from the Adriatic Sea. *Acta Adriatica* **6**(3), 1–108.

LEBOUR, M. V., 1959. The larval decapod Crustacea of tropical west Africa. *Atlantide Report* **5,** 119–143.

MANNING, R. B., and HOLTHUIS, L. B., 1981. West African Brachyuran Crabs (Crustacea: Decapoda). *Smithsonian Contributions to Zoology* **306,** 1–379.

MARTIN, J. W., TRUESDALE, F. M., and FELDER, D. L., 1985. Larval development of *Panopeus bermudensis* Benedict and Rathbun, 1891 (Brachyura, Xanthidae) with notes on zoeal characters in xanthid crabs. *Journal of Crustacean Biology* **5,** 84–105.

MENON, M. K., 1937. Decapod larvae from the Madras plankton. *Bulletin of the Madras Government Museum (Natural History Section)* **3,** 1–56.

MIERS, E. J., 1886. Report on the Brachyura collected by H.M.S. *Challenger* during the years 1873–1876. Report on the Scientific Results of the Voyage of H.M.S. *Challenger* during the years 1873–76. *Zoology* **17,** xli + 362 pages, pls. 1–29.

PAULA, J., 1987. Planktonic stages of brachyuran crabs from the south-western Iberian coast (Crustacea, Decapoda, Brachyura). *Journal of Natural History* **21,** 717–756.

QUINTANA, R., 1987. Later zoeal and early postlarval stages of three dorippid species from Japan (Brachyura: Dorippidae: Dorippinae). *Publications of the Seto Marine Biological Laboratory* **32**(4/6), 233–274.

RATHBUN, M. J., 1937. The oxystomatous and allied crabs of America. *United States National Museum Bulletin* **166,** vi + 278 pages, figs. 1–47, pls. 1–86.

RICE, A. L., 1980a. The first zoeal stage of *Ebalia nux* A. Milne Edwards, 1883, with a description of the zoeal characters of the Leucosiidae (Crustacea, Decapoda, Brachyura). *Journal of Natural History* **14,** 331–337.

RICE, A. L., 1980b. Crab zoeal morphology and its bearing on the classification of the Brachyura. *Transactions of the Zoological Society of London* **35,** 271–424.

RICE, A. L., and Williamson, D. I., 1977. Planktonic stages of Crustacea Malacostraca from Atlantic seamounts. "*Meteor*" *Forschungsergebnisse* **26,** 28–64.

TERADA, M., 1981. Zoeal development of three species of crab in the subfamily Dorippinae. *Zoological Magazine* **90,** 21–32.

WILLIAMS, A. B., 1984. *Shrimps, Lobsters, and Crabs of the Atlantic coast of the Eastern United States, Maine to Florida.* Smithsonian Institution Press, Washington, D.C. xviii + 550 pages.

WILLIAMSON, D. I., 1982. The larval characters of *Dorhynchus thomsoni* Thomson (Crustacea, Brachyura, Majoidea) and their evolution. *Journal of Natural History* **16,** 727–744.

WILLIAMSON, H. C., 1915. Decapoden I. Teil (Larven). *Nordisches Plankton*, 18th Lief. **6,** 557–561.