

**Description of some planktonic larval stages
of *Stenopus spinosus* Risso, 1826:
Notes on the genus and the systematic position
of the Stenopodidea as revealed by larval
characters***

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SUMMARY: Descriptions are given of some zoeal stages (I-V) of *Stenopus spinosus* Risso 1826 (Crustacea, Decapoda: Stenopodidea) from plankton collected off the Algerian coast. These larvae are compared to the same species but from other localities. They show great diversity in general appearance: in the same genus there is a wide range of detailed structure in almost all species. The genus *Stenopus* Latreille has a circumtropical distribution and the Atlantic Mediterranean species, *Stenopus spinosus*, and the Indopacific one, *Stenopus hispidus*, are vicariant, relicts from the Mesogean Sea. From a taxonomic point of view, the Stenopodidea constitute a group with doubtful affinity. From a larval point of view the form and the structure of the telson is considered very important particularly the second spine reduced to a fine hair. This hair-like second telson process is not present in any Dendrobranchiata, Caridea, Astacidea and Palinura, but it is common in Stenopodidea, Thalassinidea and Anomura; there appears to be some larval affinities with reptant groups. The Stenopodidea should be considered as an independent group branching off the line which later gave rise to the Thalassinidea and Anomura. It seems likely that the origin and affinities of Stenopodidea should be found among reptant groups.

Key words: Stenopodidea, larvae, systematics, Algerian coast.

RESUMEN: DESCRIPCIÓN DE ALGUNOS ESTADOS LARVARIOS PLANCTÓNICOS DE *Stenopus spinosus* RISSO 1826: NOTAS SOBRE EL GÉNERO Y POSICIÓN SISTEMÁTICA DE LOS STENOPODIDEA ATENDIENDO A CARACTERES LARVARIOS. — Se describen las larvas de *Stenopus spinosus* Risso, capturadas con el plancton de las costas argelinas. Entre ellas, existen diferencias de detalle más o menos acusadas. Los Stenopodidea presentan numerosas variaciones de estructura en casi todas las especies dentro de un mismo género. El género *Stenopus* Latreille tiene una repartición circumtropical y *S. spinosus* (especie atlanto-mediterránea) y *S. hispidus* (especie indo-pacífica) son especies supletorias, restos del antiguo Mar Mesogeo. Desde el punto de vista taxonómico, los Stenopodidea constituyen un grupo cuyas afinidades son inciertas, en tanto que, desde el punto de vista larval, tiene mucha importancia el armazón del telson y, particularmente, la segunda espina, reducida a un pelo. Esta segunda seda no aparece en los Dendrobranchiata, Caridea, Astacidea y Palinura, pero está presente en los Stenopodidea, Thalassinidea y Anomura. Los Stenopodidea constituyen un grupo distinto, que divergió de la descendencia que, más tarde, dio nacimiento a los Thalassinidae y a los Anomura. Parece que los orígenes y las afinidades de los Stenopodidea se encuentran entre los grupos tradicionalmente considerados reptantes.

Palabras clave: Stenopodidea, larvas, sistemática, costas argelinas.

INTRODUCTION

Stenopodidea have only one family, the Stenopodidae Huxley, 1879, which has many genera: *Stenopus* Latreille, 1819, *Richardina*, A. Milne Edwards,

1881, *Spongicoloides* Hansen, 1908, *Spongicola* De Haan, 1844, *Microprosthemina* Stimpson, 1860, *Odonotozoma* Holthuis, 1946 and *Engystenopus* Alcock and Anderson, 1804.

Larval development is known in the species *Ste-*

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nopus hispidus (Olivier) (GURNEY, 1936; LÉBOUR, 1941) and recently *Microprosthemis semilaeve* (Von Martens) (RAJE & RANADE, 1978). GURNEY (1936) and LÉBOUR (1941) described 12 species of Atlantic planktonic larvae, and WILLIAMSON (1976b) described another 5 larval species from the plankton taken during the International Indian Ocean Expedition (I.I.O.E.).

CANO (1891) ascribed to *Stenopus spinosus* stages I, III and a penultimate larva collected in the plankton off Naples (Italy); KURIAN (1956) made descriptions of two zoeal stages from the eastern Adriatic Sea and BOURDILLON-CASANOVA (1960) illustrated a stage I larva from the Gulf of Lion (Marseille), both of the same species.

The five larval stages of *Stenopus spinosus* described in this paper have not been reared in captivity but were collected in surface plankton hauls off the Algerian coast. These larvae are compared to those which have been ascribed to the same species but from different localities and which show a great diversity in general appearance.

Adults are usually confined to shallow water; their larvae are often taken in the open ocean in very deep water. WILLIAMSON (1970) made some suggestions on teleplanic development of *Stenopus hispidus* as defined by SCHELTEMA (1971) for Gasteropod larvae.

The objective of this paper is to give detailed descriptions of each larval stage and to discuss the taxonomy of the Stenopodidae mainly in relation to the larval evidence.

MATERIAL AND METHODS

Larvae were collected in surface plankton hauls off the Algerian coast above great depths (600 to 2500 m), from the western part of Algiers to the eastern region, El Kala (La Calle), on the Algero-Tunisian border and mainly in summer 1973.

They were caught using the modified Juday-Bogorov and the FAO standard nets. Immediately the plankton samples were preserved with 10 % formaldehyde. All the Decapod Crustacean larvae were sorted and conserved in a solution of 15 % ethylene glycol, 2 % formaldehyde and distilled water.

To make the morphologic observations clearer and easier we used lactic acid. All drawings were made with a Leitz stereomicroscope and an American optical microscope, both with a grid square.

DESCRIPTIONS

Zoea I (fig. 1)

Carapace and rostrum (Fig. 1a) translucent. Rostrum long, about twice the carapace length and armed distally; eyes sessile. Abdomen (Fig. 1g) of 5 somites and telson; the sixth still fused to the telson. Somites 1-4 with pleural expansions; somite 1 with very small dorsal spines. Somite 3 with very long medio-dorsal spine and one stiff hair under it. Somite 4 with one long, one medium and one short stiff hairs. Somite 5 with one ventral curved and one medio-dorsal spines.

Telson (Fig. 1h) a triangular shape with 8 spines decreasing in size on each outer side. Posterior edge (Fig. 1h, h') convex with a deep notch. Total of 7 + 7 telson processes: outermost a fairly large spine with 7 antero-dorsal stiff hairs; the second hair-like with 9 stiff hairs on its mid-dorsal surface and a forked end.

Antennule (Fig. 1a) a long unsegmented peduncle reaching to about half length of rostrum, bearing at distal end, one stout inner spine and a distal segment with two short setae.

Antenna (Fig. 1a) with an endopod armed distally with two long setae. Exopod as long as the antennular peduncle with 4 segments at the end and 9 long setae on inner and distal margins and one short seta on the external side.

Maxillule (Fig. 1b) with a vestigial palp. Coxal endite with 3 terminal spines, 3 stout setae, one smaller and one medium submarginal spines. Basal endite with 3 terminal spines, the median one armed with spinules and 2 setae.

Maxilla (Fig. 1c): Basal endite with 2 distinct lobes with 4 + 4 marginal setae; coxal endite with 2 partly fused lobes with 3 + 8 marginal setae. Scaphognathite with 4 marginal and one posterior setae. Endopod unsegmented with 3 terminal setae.

Maxilliped 1 (Fig. 1d): Basis with 10 inner plumose setae placed 2 + 3 + 2 + 3 respectively. Exopod tipped with 4 plumose natatory setae. Endopod of 2 segments with 2 setae on proximal segment and 1 + 3 on distal one.

Maxilliped 2 (Fig. 1e): Basis with 2 + 1 inner setae. Exopod long with 6 terminal plumose setae. Endopod of 5 segments with respectively 2 + 1 + 0 + 2 + 5 (4 terminal, 1 dorsal) setae.

Pereiopod 1 (Fig. 1f): Endopod unsegmented with two terminal, 3 inner setae (one arising near proximal part).

Zoea II (fig. 2)

Carapace with 2 stout supra-orbital spines; ros-

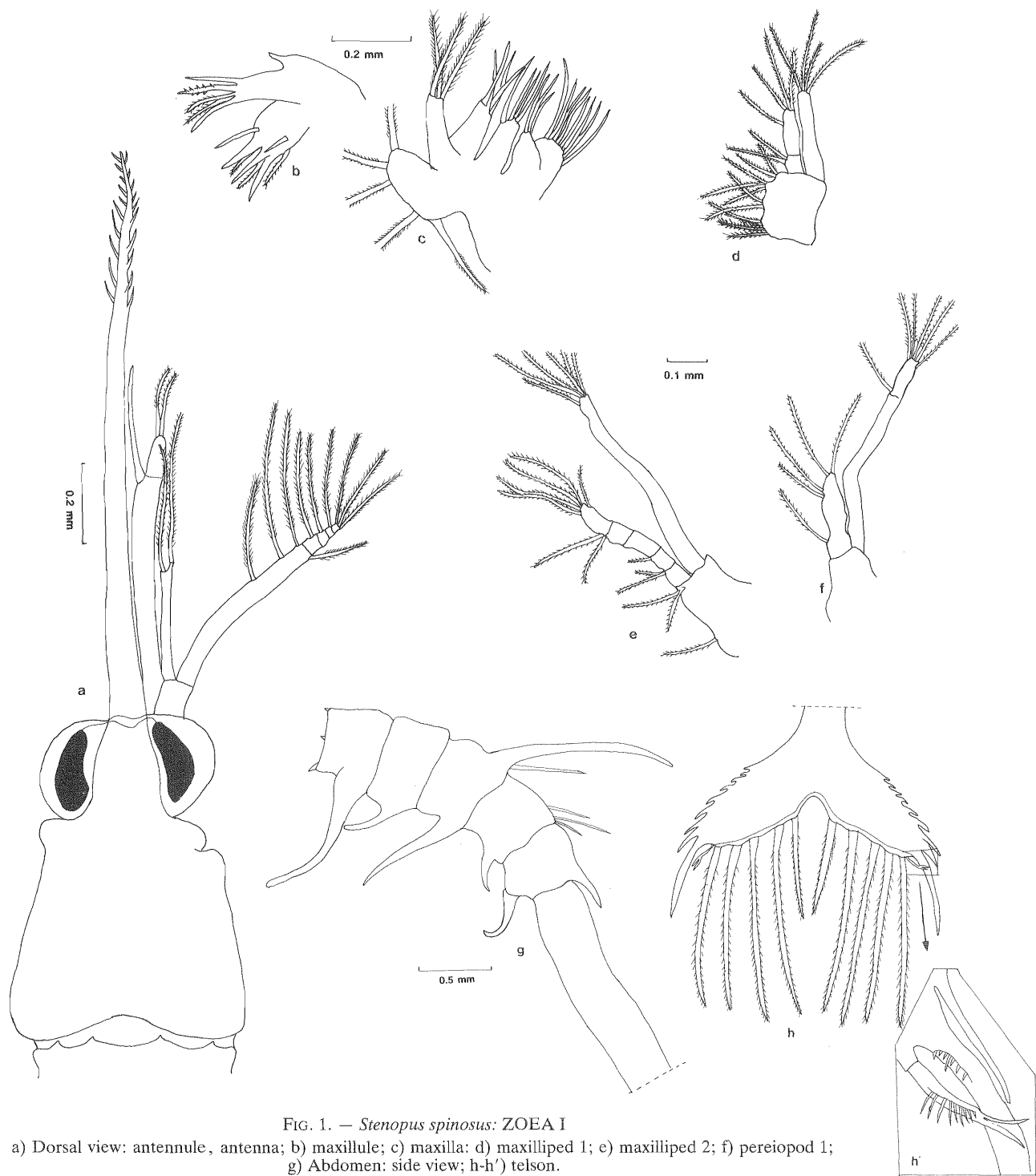


FIG. 1. — *Stenopus spinosus*: ZOEAE I

a) Dorsal view: antennule, antenna; b) maxillule; c) maxilla; d) maxilliped 1; e) maxilliped 2; f) pereiopod 1; g) Abdomen: side view; h-h') telson.

trum long about twice the antennular peduncle and armed (Fig. 2a). Eyes movable on short stalks.

Abdomen (Fig. 2b). Abdominal somites are similar to those of previous stage. But, first somite bears additional pair of rounded latero-anterior spines.

Telson (Fig. 2c) now with total of 8 + 8 marginal

processes. The second hair-like is similar to the first zoea.

Antennule (Fig. 2a) with a long unsegmented peduncle; exopod very short with 4 long plumose setae on distal margin. Endopod is a long seta. 4 small aesthetaes located medially on distal peduncle segment.

Antenna (Fig. 2a) additional small spine at inner

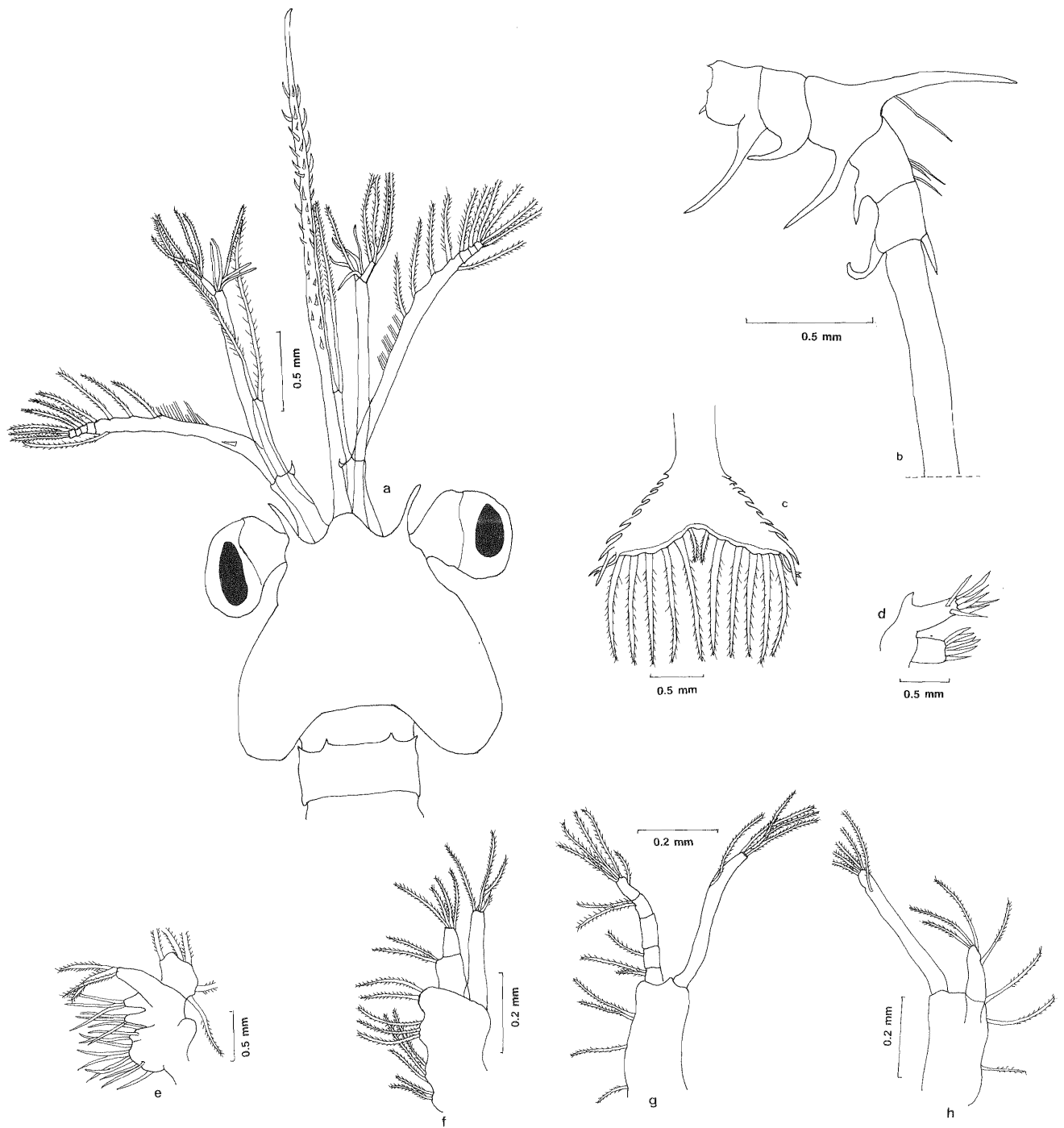


FIG. 2. — *Stenopus spinosus*: ZOEAE II

a) Dorsal view: antennule, antenna; b) Abdomen: side view; c) telson; d) maxillule; e) maxilla; f) maxilliped 1; g) maxilliped 2; h) pereiopod 1.

angle of peduncle. Exopod still segmented distally with 10 long plumose setae (3 on the distal 6 on the inner and 1 on the outer margins) and many very fine hairs on its inner margin. A small sub-marginal spine near the proximal part. Endopod little changed.

Maxillule (Fig. 2d) with vestigial palp. Coxal

endite with 6 strong spines; basal endite with 5 terminal and 2 sub-marginal spines.

Maxilla (Fig. 2e): Coxal endite partly fused with 3 + 8 setae; basal endite with 3 + 3 setae. Scaphognathite similar to the previous stage. Endopod unsegmented with 3 terminal setae.

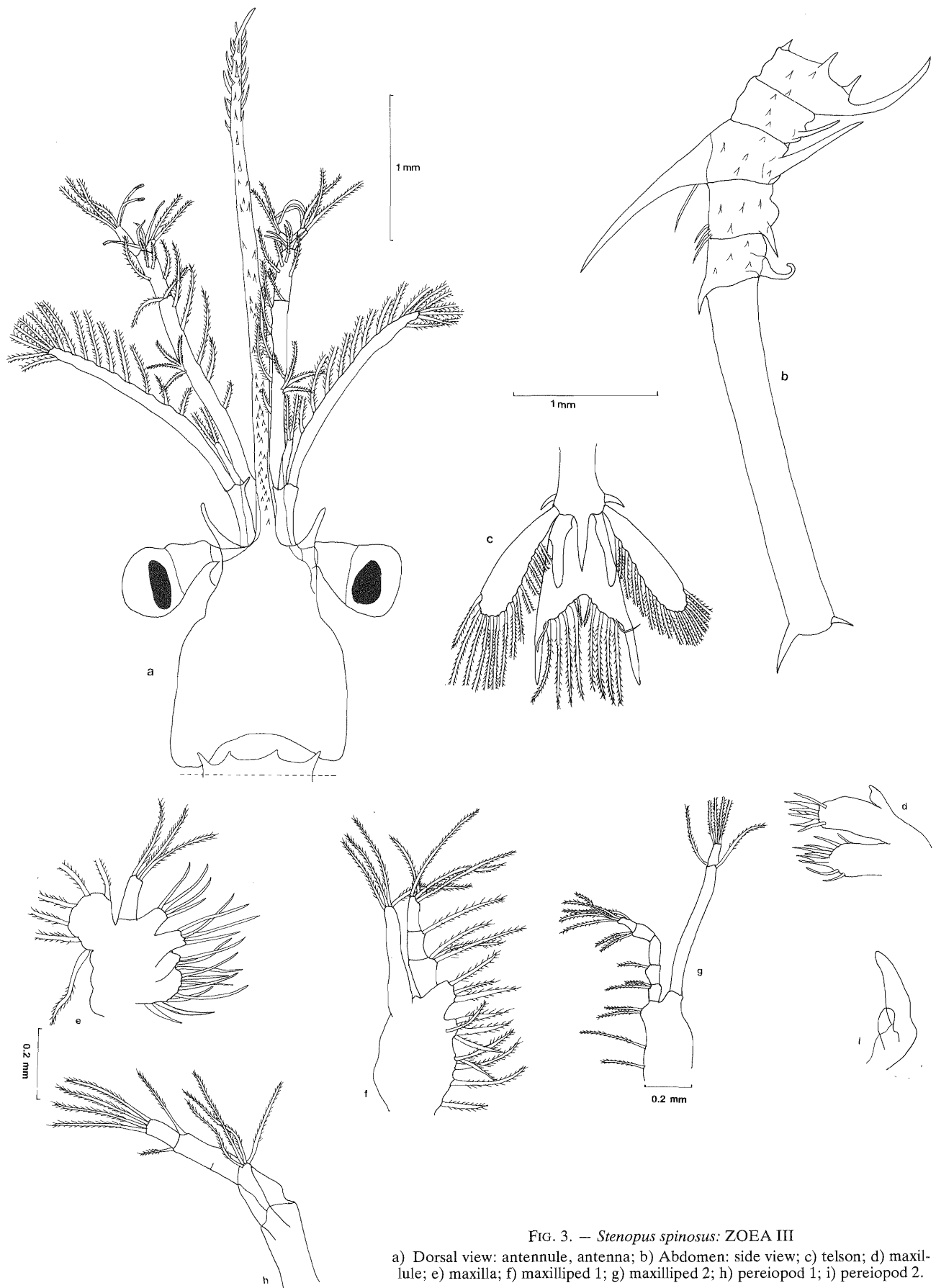


FIG. 3. — *Stenopus spinosus*: ZOEAE III

a) Dorsal view: antennule, antenna; b) Abdomen: side view; c) telson; d) maxillule; e) maxilla; f) maxilliped 1; g) maxilliped 2; h) pereiopod 1; i) pereiopod 2.

Maxilliped 1 (Fig. 2f): Inner margin of basis of respectively 2 + 3 + 3 + 2 setae. Exopod with 3 long and 1 short setae. Endopod two-segmented with 2 setae on proximal segment and 4 terminal setae on distal one.

Maxilliped 2 (Fig. 2g): Basis with 2 + 1 + 1 setae. Exopod with 4 terminal and 1 inner setae. Endopod of 5 segments with respectively 2 + 1 + 0 + 2 + 5 (4 terminal, 1 dorsal) setae.

Pereiopod 1 (Fig. 2h): Basis with 3 setae. Exopod with 4 terminal and 1 sub-marginal setae. Endopod arising from anterior third of basis, unsegmented with 3 terminal and 1 sub-marginal setae.

Pereiopod 2 presents as a bud but not represented.

Zoea III (fig. 3)

Carapace, rostrum (Fig. 3a) and supra-orbital spines similar to the previous stage. Eyes on slightly longer stalks.

Abdomen (Fig. 3b). Somite 6 separated from telson with a stout dorsal curved and 2 short postero-lateral spines. Somite 1-5 with spinules. The latero-anterior and dorso-anterior spines of somite 1 stronger.

Telson (Fig. 3c). Parallel-sided with a V shaped posterior edge with 7 + 7 marginal processes, including stout outer spines and hair-like second process on each side. The second fine hair bears very short stiff hairs.

Antennule (Fig. 3a) slightly longer; peduncle of two segments: proximal segment long, bears 5 inner setae, a group of 4 outer and 2 terminal setae; distal segment short with one inner, one outer and 2 sub-marginal setae. Endopod very short with 2 terminal setae. Exopod slightly longer with 3 long terminal setae and 2 short aesthetascs. 2 long and 2 short aesthetascs located medially on distal peduncle segment.

Antenna (Fig. 3a). Peduncle unchanged. Exopod distally unsegmented with 15 long setae (4 terminal, 1 outer, 10 inner margins). Endopod little changed.

Maxillule (Fig. 3d) unchanged.

Maxilla (Fig. 3e) unchanged except that scaphognathite now bears 6 plumose setae.

Maxilliped 1 (Fig. 3f). Inner margin of basis now with 12 setae. Exopod with 4 terminal natatory setae. Endopod of 3 segments with respectively 3 + 1 + 4 setae.

Maxilliped 2 (Fig. 3g). Basis and endopod unchanged. Exopod of 2 segments: Proximal segment with 1 + 1 distal setae; distal segment with 4 terminal setae.

Pereiopod 1 (Fig. 3h). Endopod arising from anterior third of basis, unsegmented with 4 long terminal setae. Exopod of 2 segments: Proximal

segment with 1 short + 1 long setae at distal part; distal segment with 4 long terminal setae.

Pereiopod 2 (Fig. 3i). Biramous, without setae; not functional.

Pereiopod 3 presents as a bud but not represented.

Uropods now present (Fig. 3c): Biramous; endopod without setae. Exopod with 15 plumose setae.

Zoea IV (fig. 4)

Carapace, rostrum unchanged and not represented.

Abdomen (Fig. 4b). Unchanged somites except for loss of stiff hairs on third abdominal somite and shorter second and fourth pleural expansions.

Telson (Fig. 4c) longer, parallel-sided; posterior edge with 3 + 1 + 1 + 3 setae and 1 + 1 outermost spines.

Antennule (Fig. 4a). Little changed: Proximal peduncle segment with 7 inner plumose + 4 terminal setae and 4 fine setae and 1 sub-marginal spine on mid-outer margins; distal peduncle segment with some spinules, 4 sub-marginal and 3 outer + 2 inner marginal setae. Exopod with 3 terminal and 1 lateral setae. Endopod short and conical with 1 long terminal seta. Between exopod and endopod 3 aesthetascs.

Antenna (Fig. 4a). Peduncle with 1 stout inner marginal spine. Endopod short with 2 long and 1 short terminal setae and 1 fairly long outer marginal seta. Exopod unsegmented with 12 inner marginal setae, 4 terminal and 1 outer marginal setae.

Maxillule (Fig. 4d). Unchanged.

Maxilla (Fig. 4e). Little changed.

Maxilliped 1 (Fig. 4f). Little changed.

Maxilliped 2 (Fig. 4g). Little changed.

Pereiopod 1 (Fig. 4h). Little changed.

Pereiopod 2 (Fig. 4i). Endopod with 2 terminal and 1 sub-marginal setae.

Pereiopod 3 (Fig. 4j). Biramous but not functional.

Pereiopod 4 as a bud but not represented.

Uropods (Fig. 4c). Protopod with stout spine at each angle. Exopod with a stout outermost spine and 19 marginal and 1 sub-marginal setae. Endopod with 12 marginal setae and 1 sub-marginal spine.

Zoea V (fig. 5)

Carapace, rostrum unchanged and not represented.

Abdomen (Fig. 5b, b'). 6 abdominal somites with spinules. Somite 1 with stout dorso-anterior and latero-anterior spines. Somite 4 with 2 long and 4 short dorsal stiff hairs. The sixth bears a series of lateral denticulations and a pair of long hairs near postero-lateral spine; dorsal spine longer.

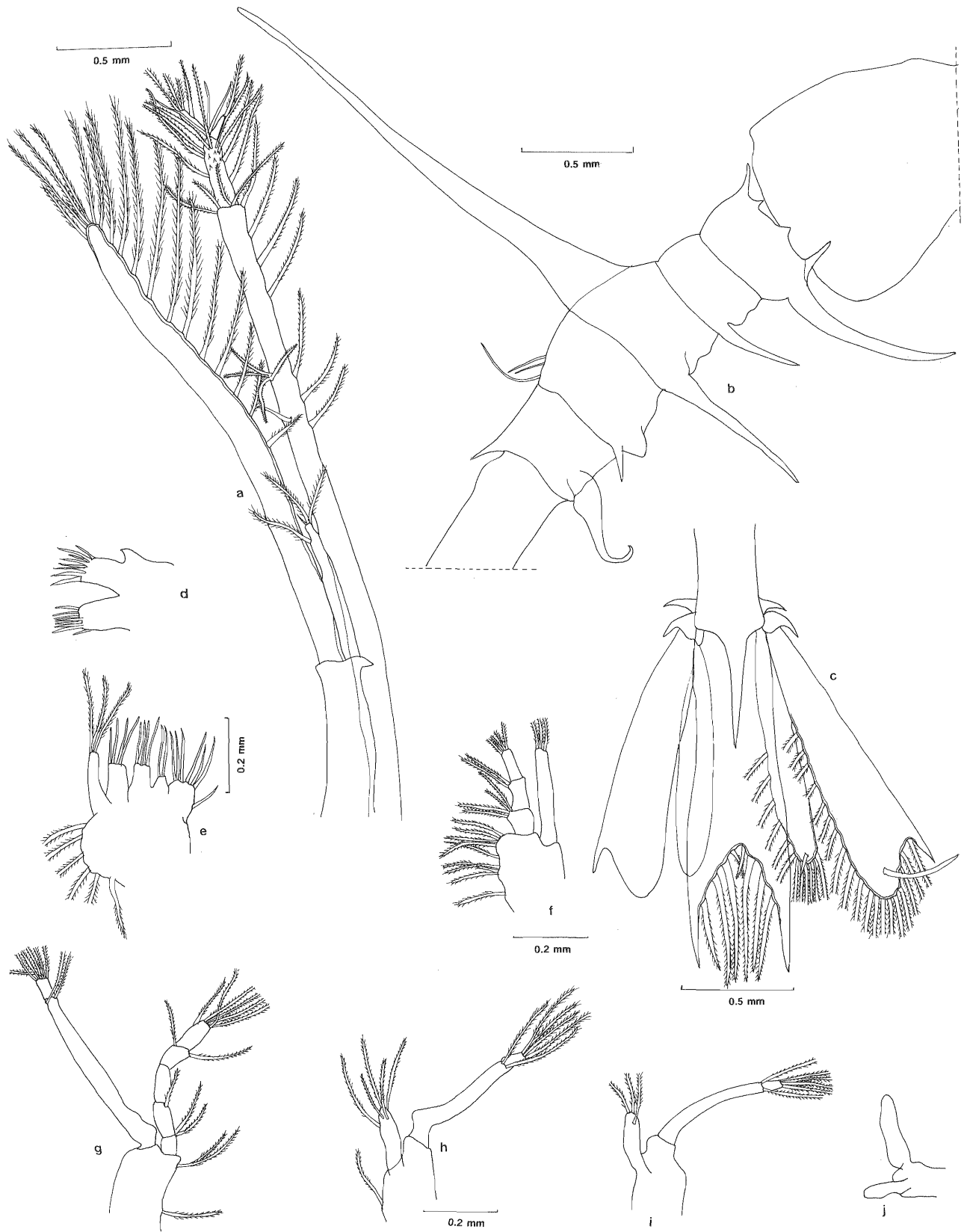


FIG. 4. — *Stenopus spinosus*: ZOEIA IV
 a) Antennule, antenna; b) Abdomen; side view; c) telson; d) maxillule; e) maxilla; f) maxilliped 1; g) maxilliped 2;
 h) pereiopod 1; i) pereiopod 2; j) pereiopod 3.

Telson (Fig. 5c). Longer with 3 + 1 + 3 setae on the posterior edge.

Antennule (Fig. 5a). Peduncle of 3 segments: proximal segment with 4 and a bunch of 6 outer marginal setae and 8 short setae on inner margin; middle segment with a bunch of 5 outer setae and 13 long setae decreasing in size on inner margin; distal segment with 3 inner marginal setae and 10 sub-marginal long setae. Endopod conical with a terminal seta. Exopod long and larger ending with 2 long setae, 2 lateral and 5 distal sub-marginal setae on anterior third.

Antenna (Fig. 5a). Short endopod with 3 terminal setae. Exopod shorter than antennular peduncle with 22 inner marginal setae, 4 terminal and 3 outer marginal setae.

Maxillule (Fig. 5d). Unchanged except coxal and basal endite spines with spinules.

Maxilla (Fig. 5e). Little changed. Scaphognathite with 19 marginal setae.

Maxilliped 1 (Fig. 5f). Little changed.

Maxilliped 2 (Fig. 5g). Little changed.

Pereiopod 1 (Fig. 5h). Basis with 1 marginal seta. Endopod partly segmented with 3 terminal and 1 sub-marginal setae and 1 seta near the proximal part. Exopod two-segmented: Proximal segment with 4 marginal, 2 sub-marginal setae and 1 long and two short terminal setae; distal segment with 5 terminal setae.

Pereiopod 2 (Fig. 5i). Biramous; endopod with 3 long setae.

Pereiopod 3 (Fig. 5j). Biramous: Endopod ending with two long setae.

Pereiopod 4 (Fig. 5k). Biramous but not functional.

Pereiopod 5 (Fig. 5l) as a bud.

Uropods (Fig. 5c). Little changed: Lack of outermost spine of exopod.

Pleopods: Absent.

DISCUSSION

The true number larval stages is known only in *Microprosthema semilaeve* which has been reared through 4 zoeal stages to megalopa. *Stenopus hispidus* was described under 9 zoeal stages by GURNEY (1924, 1936) and a post-larva by LEBOUR (1941); but the total number of larval stages is not known as well as in *Stenopus spinosus*. As there are no pleopod buds in stage V the number of larval stage is probably very high. In some genera such as *Spongicoloides* the

development is direct but, there are also several genera with large eggs and abbreviated larval development. WILLIAMSON (1976b) in his key of known Stenopodidea larvae, followed BOURDILLON-CASANOVA (1960) in stating that in *Stenopus spinosus* there are no pleural spines on somites 2 and 4. It is now obvious that this is not always the case. He also implied that the pleural spines on somites 1 and 3 are longer than the depth of the abdomen. This is true in the early stages, but in stage V the pleural spines on somite 1 are about equal to the depth of abdomen and shorter on somite 3. The presence of pleural spines was observed by WILLIAMSON (1976b) in species Ind. 2. But, our specimens differ in having a longer dorsal spine on the third somite and a short rostral spine.

The comparison of some zoeae described by KURIAN (1956), by BOURDILLON-CASANOVA (1960) and by us (zoea I) show some differences in detail. As only one species *Stenopus spinosus* occurs, in the Mediterranean Sea these variations should be individual. But SAINT-LAURENT & CLEVA (1981) in their study of Stenopodidea from Philippines have noticed that in the same genus there are many related forms and a wide range of structure variations in almost all species. Furthermore, the lack of information on juvenile morphology, in addition to the structural variability among adults, makes identification very difficult. Moreover, egg size varies in the same species; this seems more related to the stage of development of eggs than to intra-specific or individual variations or to the size of the female.

According to BALSS (1914) *Stenopus spinosus* has been reported from the Red Sea. But a further detailed re-examination of these Red Sea specimens by LEWINSOHN & HOLTHUIS (1978) shows that they cannot be assigned to the genus *Stenopus*. These authors refer them to *Engystenopus spinulatus* Holthuis whose female bears numerous small eggs 0.5 to 0.6 mm in diameter.

From the larval definition of *Stenopus*, WILLIAMSON (1976b) had arranged together all the larvae which resemble those *S. hispidus* and *S. spinosus* which have common features, also shared by Stenopid H. Lebour, species Ind. 1, species Ind. 2 and *Stenopus* sp Ranade. This larval grouping corresponds to adult genus, which, according to the geographic distribution, allows a link between Stenopid H. Lebour and *S. scutellatus* Rankin; species Ind. 2 and *S. zanzibaricus* Bruce; *Stenopus* sp Ranade belongs to an undescribed adult.

HOLTHUIS (1958) had earlier identified a juvenile

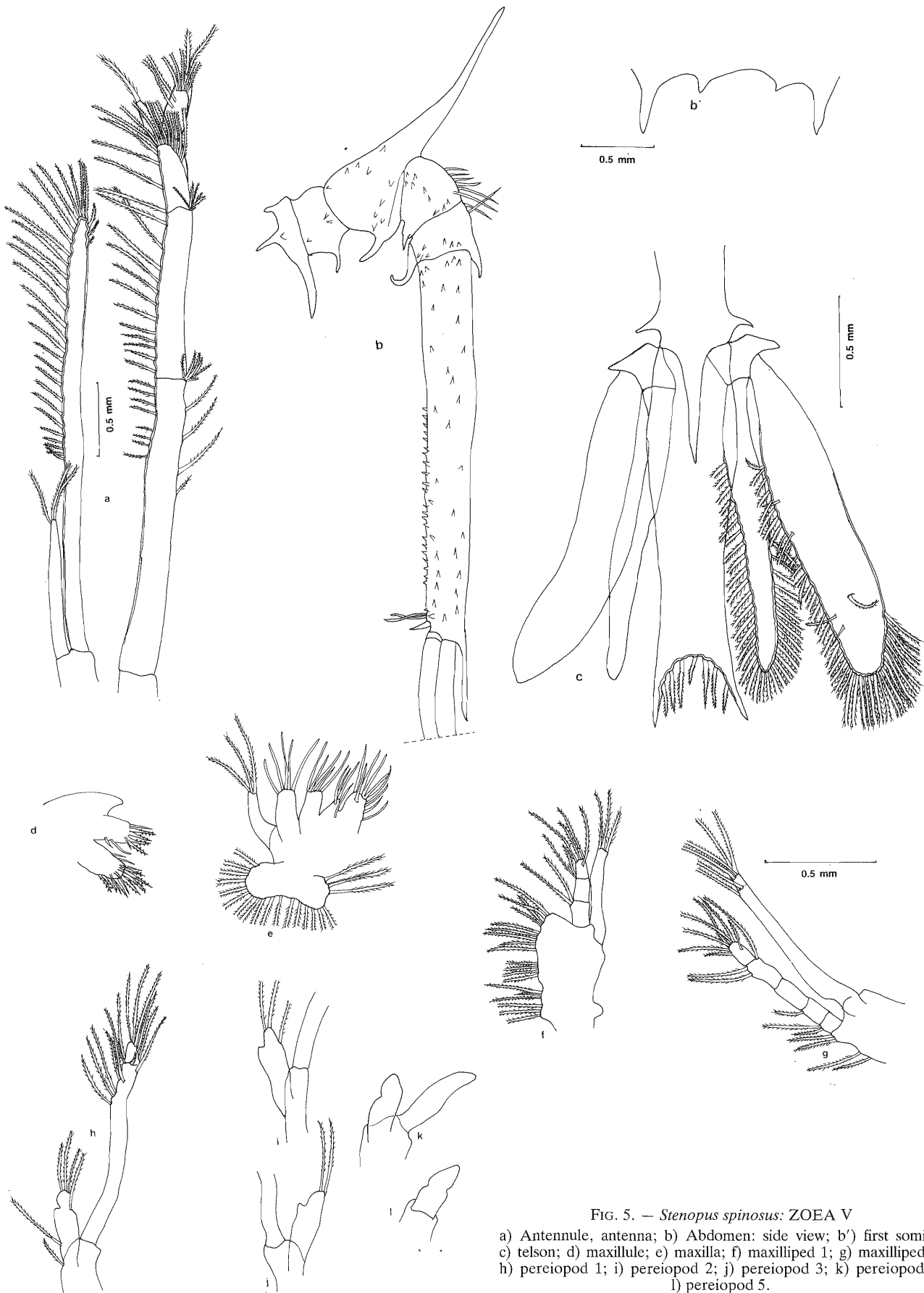


FIG. 5. — *Stenopus spinosus*: ZOEAE V

- a) Antennule, antenna;
- b) Abdomen: side view; b') first somite;
- c) telson;
- d) maxillule;
- e) maxilla;
- f) maxilliped 1;
- g) maxilliped 2;
- h) pereiopod 1;
- i) pereiopod 2;
- j) pereiopod 3;
- k) pereiopod 4;
- l) pereiopod 5.

of *S. hispidus* from the western coast of the Gulf of Aqaba and WILLIAMSON (1970) observed a late larva of the same species from the same locality. I observed (SERIDJI, 1985) larval stages I-V from the eastern coasts of Gulf of Aqaba (Jordan). *S. hispidus* is widely distributed in the Indopacific regions. The genus *Stenopus* has a circumtropical distribution and *S. spinosus* (Atlantic Mediterranean species) and *S. hispidus* (Indo-Pacific species) are vicariant species, relict from the old Mesogean Sea (PERÈS, 1985).

From the ontogenic point of view, the Stenopodidea do not hatch as nauplius nor as protozoa, but the first zoea resembles the mysis stage of Penaeoidea: Large size, long rostrum, dorsal spine on the third, the fifth, the sixth abdominal somites; these characters are most likely derived features. These larvae share also Thalassinid and Anomuran features which are present in Dromiacea: the telson shape and the second reduced spine as a fine hair or hair-like on its posterior edge (GURNEY, 1924, 1936, 1942). By these characters the Stenopodidea constitute a group with doubtful affinity.

BURKENROAD (1963) in his critical examination based upon fossil record, suggested that there are two main lines of Decapod evolution and divided them into two orders: Dendrobranchiata Bate, 1888, with Penaeoidea Raffinesque, 1815, and Sergestoidea Dana, 1852, and Pleocyemata Burkenroad, 1963, for the remaining Decapods in which he retained the two supersections: Natantia with Stenopodidea and Eukyphida (= Caridea) and Reptantia. This view was accepted by SAINT-LAURENT (1979) but, she included the Stenopodidea in Reptantia. In his most recent revision of Decapoda, almost based on the adult characters, BURKENROAD (1981) recognized four sub-orders: Dendrobranchiata, Euzygida (= Stenopodidea), Eukyphida (= Caridea) and Reptantia. The first and the last sub-order have an independent origin while the two others have a common origin.

In recent years, many zoologists have embraced the classification of Crustacea Decapoda proposed by BOWMAN & ABELE (1982). FELGENHAUER & ABELE (1983) in their comparative morphological study of Peneid, Stenopodid, Caridid and Procaridid shrimps come to the conclusion that each group represents an independent evolutionary line whereas the Caridea which are a heterogeneous group should be re-examined.

From the larval point of view, WILLIAMSON (1965, 1976a, 1982) devoted his whole attention to the telson armature and particularly to the second

reduced telson process as hair-like or fine hair. This second fine hair, as it has been said, is present only in Stenopodidea, Thalassinidea, Anomura and Dromiacea. WILLIAMSON (1965, 1976a, 1982) and RICE (1980) have assumed that the second hair-like telson process is an apomorphous character. BURKENROAD (1981) suggested that this fine hair telson process "seems to be more likely a relic feature from a common ancestral stem of the three incubatory sub-orders" (Stenopodidea, Caridea, Reptantia). The Stenopodidea do not have any adult fossil ancestor (GLAESSNER, 1969) and it is even more unlikely at the larval level. WILLIAMSON (1982) pointed out that the larvae, like the adults, are neither more nor less difficult to separate, and asked why the selection which has acted on the adult, does not act on the ontogenic development. As this second fine hair occurs neither in the Dendrobranchiata, in the Caridea, in the Astacidea, nor in the Palinura, it would be more an apomorphous feature than a simple relic. Moreover, in his recent paper, WILLIAMSON (1988) shows that the ancestral telson processes were in the form of plumed setae and there were kept by Caridea, while in the other groups of Pleocyemata the outermost pair of telson process became spini-form (zoea I). The hair-like second telson process is found in groups already quoted (see above) and Williamson considers it as "an inheritance from a single group". Consequently, the larval condition in the Stenopodidea has evolved from a primitive ancestor which had larval characters common to Thalassinidea and Anomura. Thus, the Stenopodidea form a distinctive group branching off the line which later gave rise to Thalassinidea and Anomura (Fig. 6).

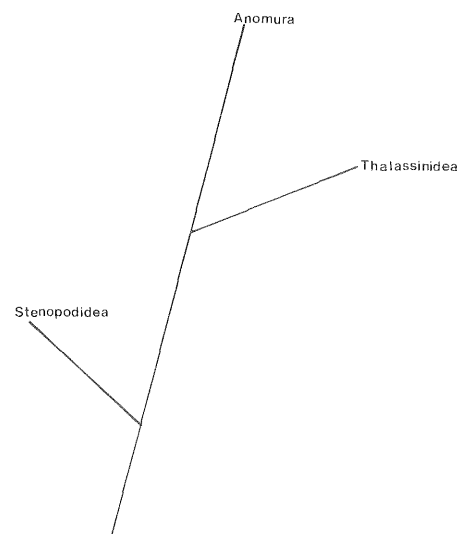


FIG. 6. — Suggested phylogeny of the Stenopodidea.

Therefore, the origin and the affinity of the Stenopodidea should be found among reptants as was suggested by FELGENHAUER & ABELE (1983).

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