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AMMOPHILA (COPEPODA : CALANOIDA)**

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## TWO RELICT TETHYAN COPEPODS NEW FOR THE MEDITERRANEAN SEA : *EXUMELLA POLYARTHRA* AND *PARAMISOPHRIA AMMOPHILA* (COPEPODA : CALANOIDA)

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COPEPOD  
*EXUMELLA*  
*PARAMISOPHRIA*  
MEDITERRANEAN  
RELICT

**ABSTRACT** – The copepod *Exumella polyarthra* Fosshagen, 1970, previously only reported from the Bahamas, has been recordered in three different submarine caves of Minorca (Balearic Islands, Western Mediterranean). Two females of *Paramisophria ammophila* Fosshagen, 1968 and two copepodids V have been also recordered. The description of the copepodid V of *Paramisophria ammophila* is included. Relationship between this interesting case of biogeographic distribution and the possible relict tethyan character of these species are discussed.

COPÉPODE  
*EXUMELLA*  
*PARAMISOPHRIA*  
MÉDITERRANÉE  
RELICTE

**RÉSUMÉ** – Les Copépodes calanoïdes *Exumella polyarthra* Fosshagen, 1970 et *Paramisophria ammophila* Fosshagen, 1968, décrits des Bahamas, ont été observés dans des grottes sous-marines à Minorque (Iles Baléares). Les caractères morphologiques sont donnés, ainsi que la description du copépodite V de *Paramisophria ammophila*. La distribution géographique et le caractère relict de ces formes en Méditerranée occidentale sont évoqués.

### INTRODUCTION

Cave faunas have drawn great attention because they are inhabited by numerous Tethyan relicts and endemic organisms (Iliffe *et al.* 1984; Wilkens *et al.* 1986; Boxshall 1989; Ohtsuka *et al.* 1993). Diverse biological communities have been found in totally or partially submerged marine caves, and several groups of high taxonomic value have been described (Sket & Iliffe 1980; Yager 1981; Iliffe *et al.* 1984; Bowman & Iliffe 1985).

A carefull examination of some cave-dwelling copepods from the Mediterranean Sea revealed the presence of some interesting species in the caves of Minorca Island.

The copepod family Ridgewayiidae M.S. Wilson, 1958 includes four genera: *Ridgewayia* Thompson & A. Scott, 1903; *Exumella* Fosshagen, 1970; *Placocalanus* Fosshagen, 1970; and *Brattstromia* Fosshagen, 1991. All the species of these genera are characteristic of shallow waters, coastal areas and submarine caves of tropical and sub-tropical regions.

The genus *Ridgewayia* includes nine species (three males not described) with a wide geographic range. The genera *Exumella* and *Placocalanus* include two species each, and the genus

*Brattstromia* is known only from the type species (Table I).

The eight genera included in the family Arietelidae G.O. Sars, 1902 are pelagic, except *Paramisophria* T. Scott, 1897 which is epibenthic and inhabitant of caves or hypersaline bays.

The present paper includes the record of *Exumella polyarthra* and *Paramisophria ammophila*, and the description of the stage V of *P. ammophila*, both species inhabiting different marine caves on Minorca Island. Their presence represents the first record for the Mediterranean Sea. A discussion of the possible relation between these Mediterranean populations and those described on the Bahamas region is also included, considering the relict character of these species and their possible origin in the Tethys Sea.

### MATERIAL AND METHODS

Samples were obtained using diving techniques, with a net of mesh size 0.250 mm and square mouth of 900 cm<sup>2</sup>. Two females and two copepodids of *Paramisophria ammophila* and 116 females, 229 males and 10 copepodids of *Exumella polyarthra* were collected in



Genus	Species	Locality
<i>Ridgewayia</i>	<i>canalis</i> (Gurney, 1927)	Suez Canal (Kabret, Ismailia)
	<i>flemingeri</i> Othman & Greenwood, 1988	Australia (Gulf of Carpentaria)
	<i>fosshageni</i> Humes & Smith, 1974	Panama, Bahamas
	<i>gracilis</i> M.S. Wilson, 1958	Florida (SW coast)
	<i>krishnaswamyi</i> Ummerkutty, 1963	Indian Ocean
	<i>marki</i> (Esterly, 1911)	Bermuda Islands (marine caves)
	<i>shoemakeri</i> M.S. Wilson, 1958	Panama, Florida
	<i>typica</i> Thompson & Scott, 1903	Ceylon
	<i>wilsonae</i> Fosshagen, 1970	Bahamas
	sp. (Krishnaswamy, 1953) sp. Yeatmann 1969	India (Madras) Bermuda Islands
<i>Exumella</i>	<i>polyarthra</i> Fosshagen, 1970	Bahamas (Exuma Islands), Minorca
	<i>tuberculata</i> Grahame, 1970	Jamaica (Kingston Harbour)
<i>Placocalanus</i>	<i>insularis</i> Fosshagen, 1970	Bahamas
	<i>namnus</i> Fosshagen, 1970	Bahamas
<i>Brattstromia</i>	<i>longicaudata</i> Fosshagen, 1991	Belize (Giant Cave, Caye Caulker)

Table I. – Geographic distribution of the species within the family Ridgewayiidae.

Table II. – Station data of the marine caves where individuals of *Exumella polyarthra* and *Paramisophria* sp. were collected.

Cave	Locality	Mean Depth (m)	Temperature (°C)
Cap d'en Font	39°49'43''N, 4°12'20''E	14	17.1
Cova Sa Gamba			
Cala'n Porter	39°52'07''N, 4°07'33''E	6	23

different marine caves on Minorca (Balearic Islands, Western Mediterranean). Station data for the specimens described here are resumed in Table II.

Samples were preserved in 5% formalin solution.

All measurements and dissections were made on specimens in lactic acid, following the method used by Humes & Gooding (1964). The length of the body does not include the caudal rami. The morphological terminology of copepods is based on Huys & Boxshall (1991), Fosshagen & Iliffe (1989).

## THE SPECIES DESCRIPTIONS

### FAMILY RIDGEWAYIIDAE M.S. Wilson, 1958

#### Genus *Exumella* Fosshagen, 1970

#### *Exumella polyarthra* Fosshagen, 1970 (Fig. 1A-E)

#### Material examined

116 adult females (38 on 19 June 88 and 75 on 30 October 82 from Sa Gamba cave; 2 on 19 June 88 from Cap d'en Font cave; and 1 on 10 July 88 from Calau Porter cave), 229 adult males (49 on 19 June 88 and 180 on 30 October 82 from Cova Sa Gamba) and 10 copepodids. Some specimens have been dissected and mounted on slides. All the samples and slides are deposited in the Laboratoire Arago (Banyuls-sur-Mer, France).

#### Adult female (Fig. 1 A-E)

The total length of 10 individuals ranged between 0.80 and 0.89 mm with an average of 0.84 mm (std = 0.035).

Some of the females (Fig. 1A-B) had a long spermatophore (Fig. 1C) reflecting a recent copulation.

No differences have been observed between the individuals of Minorca and those of Bahamas described by Fosshagen (1970). For that reason, only some appendages are represented here (Fig. 1D-E), as a complement of the description by Fosshagen (1970).

### FAMILY ARIETELLIDAE G.O. Sars, 1902

#### Genus *Paramisophria* T. Scott, 1897

#### *Paramisophria ammophila* (Fig. 2A-Q)

#### Taxonomy

Among the 8 genera included in the family Arietellidae, *Paramisophria* T. Scott, 1897 was re-described by Krishnaswamy (1959), Ohtsuka *et al.* (1991) and Ohtsuka *et al.* (1993). There are 11 species and 1 juvenile form described: *P. ammophila* Fosshagen, 1968; *P. cluthae* T. Scott, 1897; *P. fosshageni* Othman & Greenwood, 1992; *P. galapagensis* Ohtsuka, Fosshagen and Iliffe, 1993; *P. giselae* (Campaner, 1977); *P. itoi* Ohtsuka, 1985; *P. japonica* Ohtsuka, Fosshagen & Go, 1991; *P. platysoma* Ohtsuka & Mitsuzumi, 1990; *P. reducta* Ohtsuka, Fosshagen and Iliffe, 1993; *P. spooneri* Krishnaswamy, 1959; *P. variabilis* McKinnon & Kimmerer, 1985; *Paramisophria* sp. Ohtsuka, Fosshagen & Go, 1991. The species described by Tanaka (1966) as *P. cluthae* is different from that described by T. Scott (1897). Nevertheless, as all the authors have emphasized, it is difficult to consider it as a different species from *P. cluthae* T. Scott, 1897 because of the absence of males. *P. cluthae* T. Scott, 1897, described from Lake Fyne (Scotland), was found later by Sars (1902) near the west coast of Norway. It was reported also by Sars (1925) from



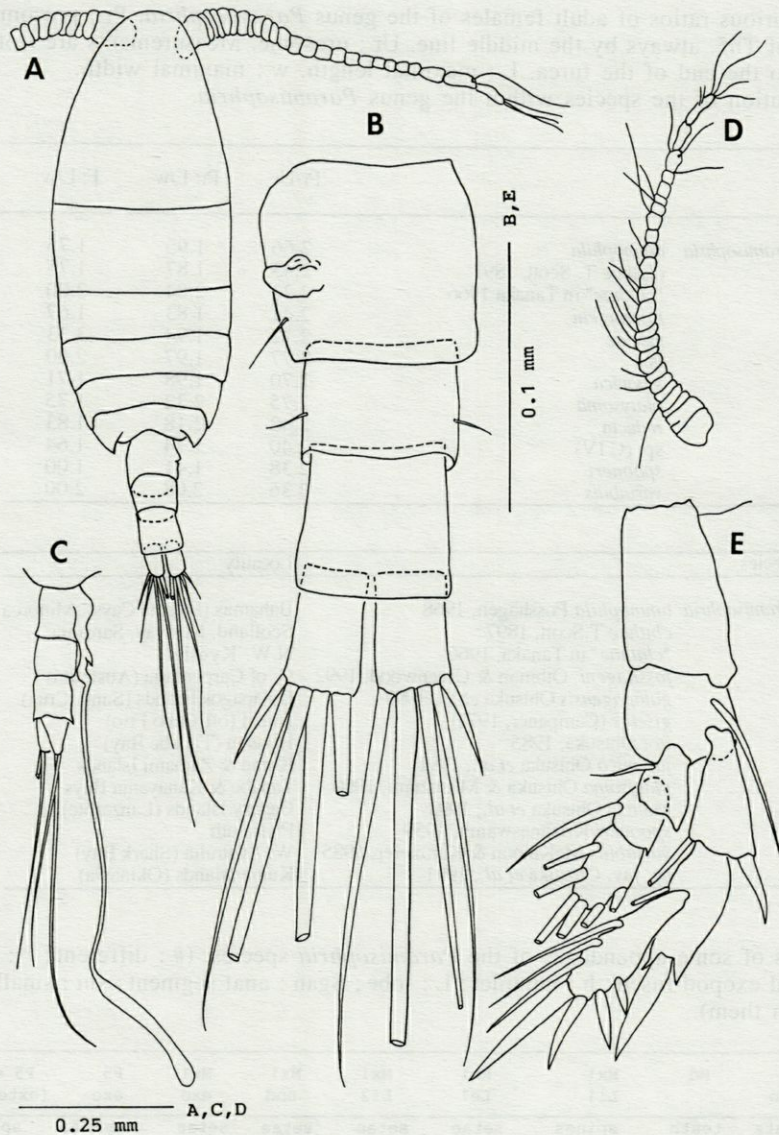


Fig. 1. - *Exumella polyarthra* Fosshagen, 1970, adult female. A, Dorsal view. B, Urosome in ventral view. C, lateral view of the spermatophore and urosome. D, Antennule (A1). E, Fifth leg.

Sardinia (Porto Conte) and by Tanaka (1966) from the coastal waters of the north-west coast of Kyushu (Japan).

The different proportions of the body and the furca of all the species of *Paramisophria* having been described so far are included in Table III A. Their geographical distribution is summarized in Table III B.

#### Material examined

2 females and 2 female copepodids were re-recorded from Sa Gamba cave, 30 Oct. 88. All are deposited in the Laboratoire Arago (Banyuls-sur-Mer, France).

#### Female copepodid stage V (Fig. 2A-J, 3 A-E)

Body (Fig. 2A) Total length = 1.20-1.22 mm; Prosome (length/width) = 2.03-2.09; ratio of length of Prosome/Urosome = 2.51.

Head (Fig. 2B): rounded (dorsal view); rostrum invisible from dorsal view, with two filaments.

Antennule (Fig. 2C): short, extends to approximately half the cephalosome; 21-segmented, the first segment elongated.

Antenna (Fig. 2D): exopod with 4 segments.

Mouth appendages (see Remarks, Table IV and Figs. 2E-H).



Table III A. – List of various ratios of adult females of the genus *Paramisophria*. Pr : prosome. Measures forehead to the posterior margin of Th5, always by the middle line. Ur : urosome. Measurements are from the anterior margin of the genital segment to the end of the furca. L : maximal length. w : maximal width.

B. – Geographic distribution of the species within the genus *Paramisophria*.

A		Pr/Ur	Pr: L/w	F: L/w
<i>Paramisophria</i>	<i>ammophila</i>	2.66	1.95	1.75
	<i>cluthae</i> T. Scott, 1897	2.43	1.87	1.75
	" <i>cluthae</i> " in Tanaka 1966	2.22	2.04	2.00
	<i>fosshageni</i>	2.41	1.83	1.67
	<i>giselae</i>	2.12	1.94	3.33
	<i>itoi</i>	2.77	1.97	2.00
	<i>japonica</i>	2.70	1.98	1.71
	<i>platysoma</i>	2.75	2.32	1.75
	<i>reducta</i>	2.48	2.18	1.83
	sp. (C IV)	2.40	1.74	1.64
	<i>spooneri</i>	2.38	1.41	1.00
	<i>variabilis</i>	2.36	2.08	2.00

B		Locality
<i>Paramisophria</i>	<i>ammophila</i> Fosshagen, 1968	Bahamas (Exuma Cays), Minorca
	<i>cluthae</i> T. Scott, 1897	Scotland, Norway, Sardinia
	" <i>cluthae</i> " in Tanaka, 1966	N.W. Kyushu
	<i>fosshageni</i> Othman & Greenwood, 1992	G. of Carpentaria (Australia)
	<i>galapagensis</i> Ohtsuka <i>et al.</i> , 1993	Galapagos Islands (Santa Cruz)
	<i>giselae</i> (Campaner, 1977)	Brazil (off Cabo Frio)
	<i>itoi</i> Ohtsuka, 1985	Honshu (Tanabe Bay)
	<i>japonica</i> Ohtsuka <i>et al.</i> , 1991	Kume & Zamami Islands
	<i>platysoma</i> Ohtsuka & Mitsuzumi, 1990	Tanabe & Kanayama Bays
	<i>reducta</i> Ohtsuka <i>et al.</i> , 1993	Canary Islands (Lanzarote)
	<i>spooneri</i> Krishnaswamy, 1959	Plymouth
	<i>variabilis</i> McKinnon & Kimmerer, 1985	W. Australia (Shark Bay)
	sp. juv. Ohtsuka <i>et al.</i> , 1991	Kume Islands (Okinawa)

Table IV. Characteristics of some appendages of the *Paramisophria* species. (# : different; \* : trace of suture; ? : no data; Bexo : basipod and exopod fused; h : humplet; L : lobe; Sgan : anal segment; sm : small; vis / invis : visible; ≈ : very similar between them).

Species	A1 N. segments	A2 exo	Md teeth	Mx1 Li1 spines	Mx1 Le1 setae	Mx1 Li2 setae	Mx1 end setae	Mx1 exo setae	P5 exo segments	P5 exo (external) spines	P5 endo setae	Sgan
<i>ammophila</i>	21	4	1+h+3	4≈	5+3	0	1+1sm	3	1+*	3	1	<< Ur
<i>cluthae</i>	21	6	1+3	5≈	4+3	0	1	3	1	3	1	< Ur
<i>cluthae</i> in Tanaka 1966	21	4?/6	1+h+2	3≈	6+1	?	2sm	3	1	3	1	< Ur
<i>fosshageni</i>	21	7	1+3	4+1sm	5+2sm	0	1+1sm	3	1	3	1	< Ur
<i>giselae</i>	22	7	1+h+2	4+2sm	6+2	1 long	1	3	Bexo	2	2	± vis
<i>itoi</i>	21	6	1+3	4+1sm	5+3	0	1+1sm	3	2	3	1	<< Ur
<i>japonica</i>	22	6	1+3	4+1+1	6+2	1 acute	1+1sm	3	2+*	3	2	± vis
<i>platysoma</i>	21	6	1+h+3	4≈+1sm	6+2	0	2#	3	1	3	0	< Ur
<i>reducta</i>	22	8*	1+3	4+1+1	5+1	0	2#	3	1	2	1	< Ur
sp. (C IV)	22	6	1+3	4≈+1+1	6+2	1 long	1	3	1	3	2	invis
<i>spooneri</i>	20	2	? 3≈	5+2sm	?	1+1sm	2	1	3	1	< Ur	
<i>variabilis</i>	21	3	1+3	4≈	5+3	0	2	3	1	3	1	< Ur

Cephalosome & Th1 : separated.

Th4 & Th5 : fused.

Th5 (Fig. 2I) : posterior margins symmetrical and characteristic of the genus, with a sub-dorsal right point that in lateral view forms a large rounded indentation.

Urosome (Fig. 2J) : 4-segmented. Proportional length of urosomal segments and furca (% = 21.6 / 12 / 19.9 / 20 / F = 26.5).

Genital segment (Fig. 2K-K') : slight median anterior prominence. Spermatheca not clearly visible.



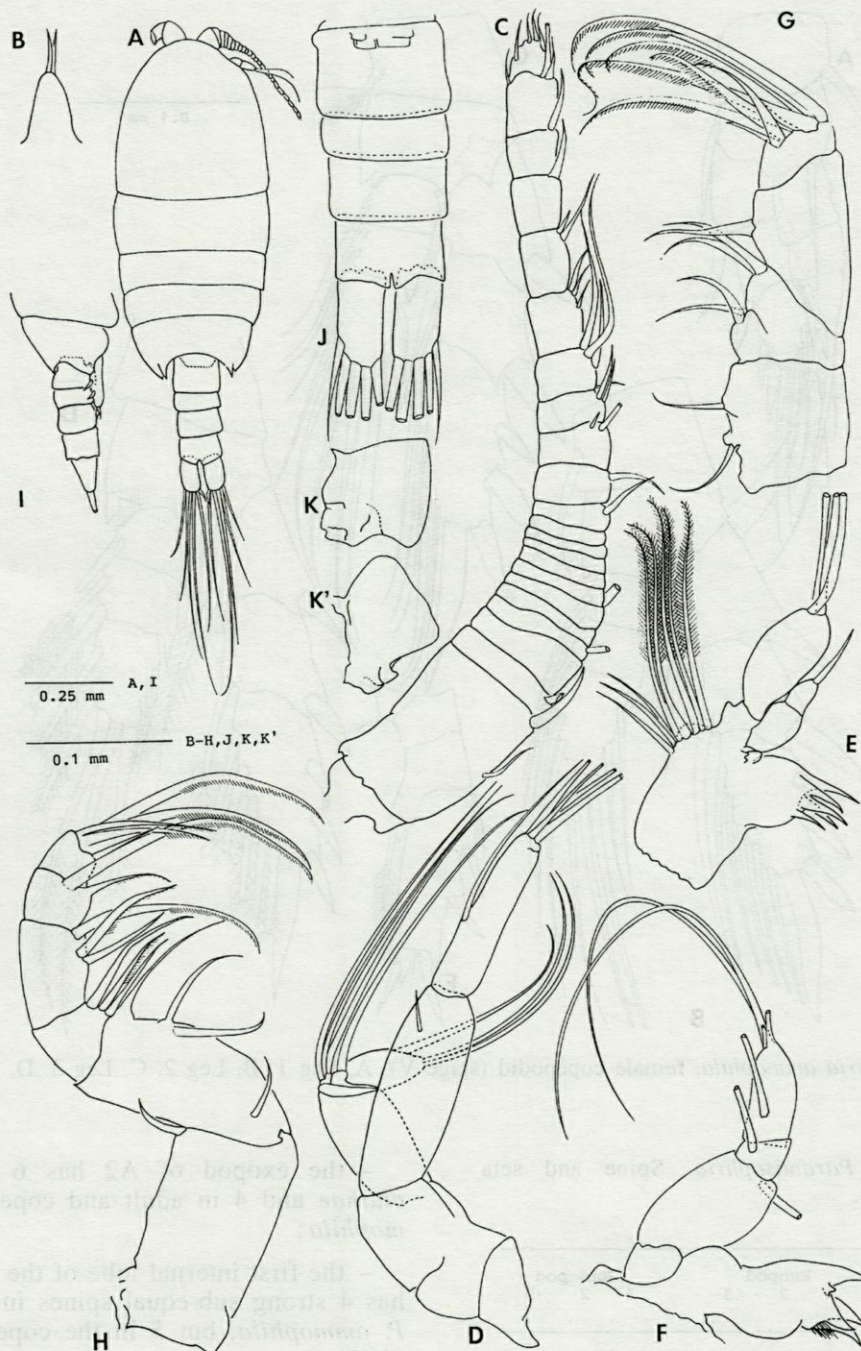


Fig. 2. - *Paramisophria ammophila*, female copepodid (stage V). A, Dorsal view. B, Rostrum. C, Antennule (A1). D, Antenna (A2). E, Maxilla 1 (Mx 1). F, mandible (Md). G, maxilla 2 (Mx 2). H, maxilliped. I, lateral view of Th 5 and urosome. J, Ventral view of the urosome. K-K', Lateral view of the genital segment.

Anal segment (Fig. 2J) : well visible, with almost the same length as the preceding segment.

Caudal rami (Fig. 2J) : asymmetrical (slightly longer on right side). Length/width ratio = 1.86 (on right side).

Legs 1-4 (Fig. 3A-D) : like those drawn by Sars (1902, Pl. 87), although there is a doubt about the presence of one setae at the basis of the leg 4 (Table V).

Leg 5 (Fig. 3E) : intercoxal sclerite visible (suture line with the coxa not well marked); coxa clearly separated from basis, which has an external setae. Endopod totally fused to basis. A fine suture is partially marked between exopodal segments 1 and 2, as hint in Fig. 2F in Fosshagen, 1968. Exopodal segment 1 has a strong spine at the distal external margin; exopodal segment 2 has only one spine near the middle of the external margin, none sub-distal.



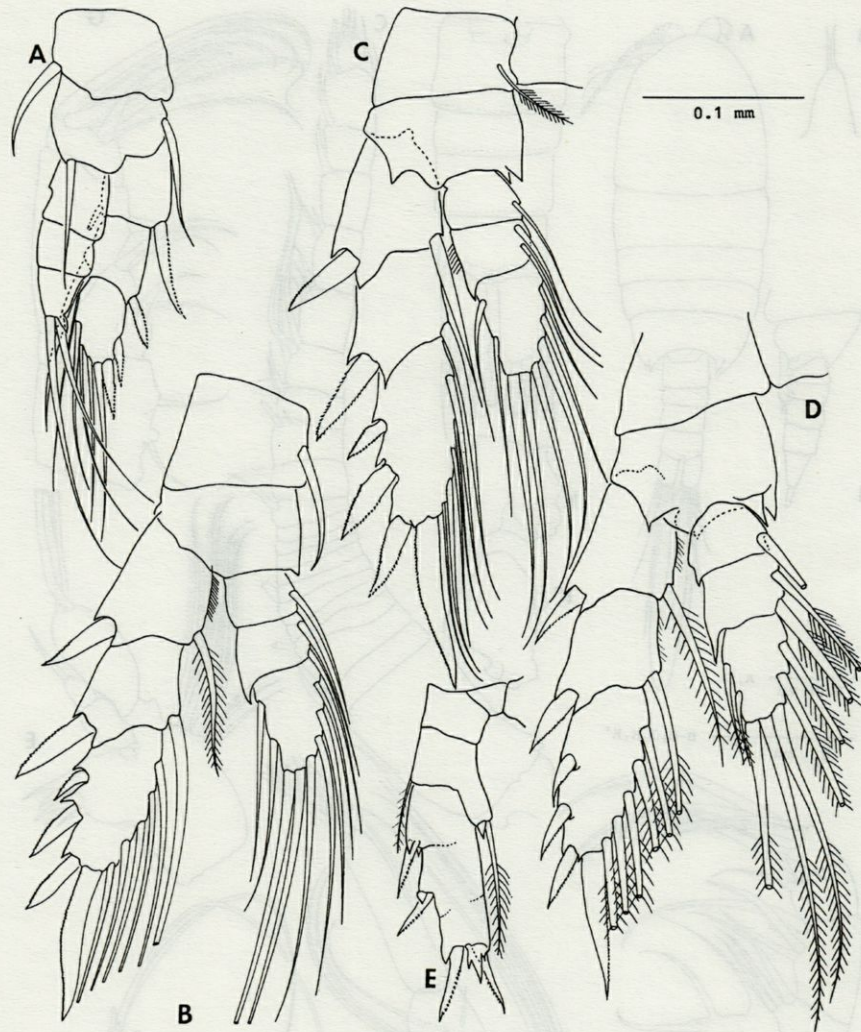


Fig. 3. – *Paramisophria ammophila*, female copepodid (stage V). A, Leg 1. B, Leg 2. C, Leg 3. D, Leg 4. E, Leg 5.

Table V. – Genus *Paramisophria*. Spine and seta formula for legs 1-4.

Leg	Coxa	Basis	Exopod			Endopod		
			1	2	3	1	2	3
Leg 1	0-1	1-1	I-1; I-1;	II-I-4		0-1; 0-2;	1-2-2	
Leg 2	0-1	0-0	I-1; I-1;	III-I-5		0-1; 0-2;	2-2-4	
Leg 3	0-1	0-0	I-1; I-1;	III-I-5		0-1; 0-2;	2-2-4	
Leg 4	0-0	1?-0	I-1; I-1;	III-I-5		0-1; 0-2;	2-2-3	

### Remarks

The most important differences between adult females of *P. cluthae*, *P. ammophila*, and the copepodid stage V of *P. ammophila* are as follows (Fig. 2, 3, 4):

– the exopod of A2 has 6 segments in *P. cluthae* and 4 in adult and copepodid of *P. ammophila*;

– the first internal lobe of the Mx1 (maxillule) has 4 strong sub-equal spines in adult female of *P. ammophila*, but 5 in the copepodid and in *P. cluthae*;

– the first external lobe of the Mx1 has 7 setae in *P. cluthae*, and 8 in the adult female and copepodid of *P. ammophila*;

– the endopod of the fifth leg has one long seta and one smaller in the adult female of *P. ammophila*, but a single long one in the copepodid and in *P. cluthae*;

– the endopod of the fifth leg is slightly longer in the adult female of *P. ammophila* than in the copepodid and in *P. cluthae*;

– the distal part of the exopod of the fifth leg of the adult female of *P. ammophila* has an external spine much longer than the inner one. In



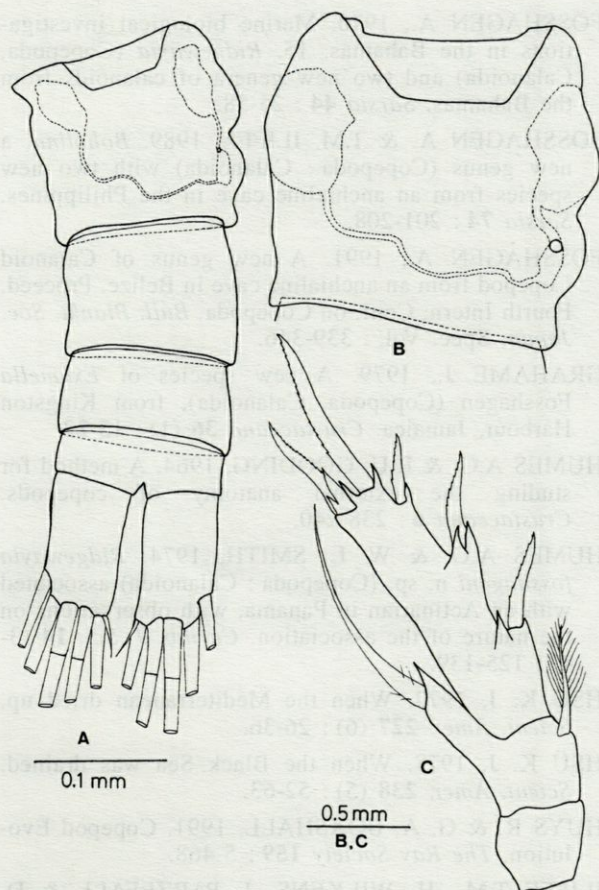


Fig. 4. *Paramisophria ammophila*, adult female. A, Ventral view of the urosome. B, Ventral view of the genital segment. C, Leg 5.

the copepodid and in *P. cluthae* both spines have similar length.

– the anal segment of the adult female of *P. ammophila* is very small compared with the preceding urosomal segment; in the copepodid and in *P. cluthae* both segments are similar in length and longer than in the adult *P. ammophila*.

– in the copepodids of *P. ammophila* the masticatory blade has a small tiny tooth at the internal basal part of the external tooth. This characteristic has been also described in the adult female of *P. ammophila*, but not in *P. cluthae*.

The only copepodid of *Paramisophria* described in the literature is that of Ohtsuka *et al.* (1991) from the Kume Islands (South Japan). It is a copepodid IV of an unknown species. The legs 1-4 have 2 segments on both the endopod and the exopod, and the fifth leg has a well separated intercoxal plate. According to these authors, the last copepodid stages are characterized by the length of the antennule, which does not extend farther than the first pedigerous segment, and by the fusion of segments in the fifth leg. In this genus the number of segments of the

antennule seems to be fixed after stage IV, as was shown by the structure of this cephalic appendage.

According to the complete number of segments of the swimming legs (Table V) the copepodid found in Minorca would correspond to an elder stage than the copepodid IV described by Ohtsuka *et al.* (1991).

## DISCUSSION

The record of *Exumella polyarthra* and *Paramisophria ammophila* from Minorca is particularly interesting from a biogeographic point of view. It not only reflects their not strictly tropical distribution, but also poses the problem of their origin.

The geographic isolation of the two populations by the Atlantic Ocean, one from the western region of the Atlantic (Bahamas) and the other from the Mediterranean Sea (Minorca), lends support to a Tethyan population with gene exchange, predating a relative narrow separation of the Atlantic Ocean. This origin followed by separation and isolation of the species by continental drift, could explain their present characteristic habitat limited to coastal and hyperbenthic areas (Table I and III).

Geologically, there are some relationships between the Caribbean and the South Spanish-Morocco areas since the continental drift and the formation of the Atlantic Ocean (Sclater & Tapscott 1979). It is plausible that the original populations of both, *Exumella polyarthra* and *Paramisophria ammophila*, inhabited the Tethys sea before the drift (200 million years ago). During the following periods (182-112 million years ago; see Dercourt *et al.* 1985) the Tethys sea began an intrusion to the Pangea, which separated Laurasia from Gondwana. The areas occupied now by the Mediterranean Sea and the Florida-Bahamas region were close and connected by that sea; this event allowed the Tethyan fauna to colonize all these regions. Posterior gradual aperture of the Atlantic (6-92 million years ago) forced the separation of the West and the East Atlantic coasts and the geographic isolation of populations at different regions. The interruption of gene flow between populations separated geographically may eventually result in the formation of evolutionarily independent units that can be recognized by genotypic differences.

For a comprehensive analysis of the biogeography of specific taxa, we do not only need data on ecology and biology of the species in question, and on the local geology and history, but also its phylogenetic relationships. Future work with molecular techniques (mtDNA, isoenzymes, or ribo-



somal RNA), would provide phylogenetic information for inferring evolutionary history.

The hypothesis of a recent origin of these species at both the western Atlantic and the Mediterranean Sea would have required convergent evolution to produce the same species in both regions. The chance of convergence producing such similarity is unlikely. Since more species of different groups show the same distribution than these two copepods cited in this manuscript (see Iliffe *et al.* 1984), the hypothesis of the Tethyan origin followed by separation and isolation of the species by continental drift is the most plausible explanation.

The Miocene partial drying of the Mediterranean (Hsü 1972, 1978) could have caused the extinction of some of the species from the open sea. Nevertheless, those inhabiting deep basins which did not dry, and perhaps also caves, could have survived.

New prospections and discoveries in different places are required to make a satisfactory analysis. By the moment, all considerations remain partially speculative.

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