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Paper/article Danielopol DL, Rouch R & Baltanas A, 2002. Taxonomic diversity of groundwater Harpacticoida (Copepoda, Crustacea) in southern France. *Vie Milieu* 52(1): 1-15
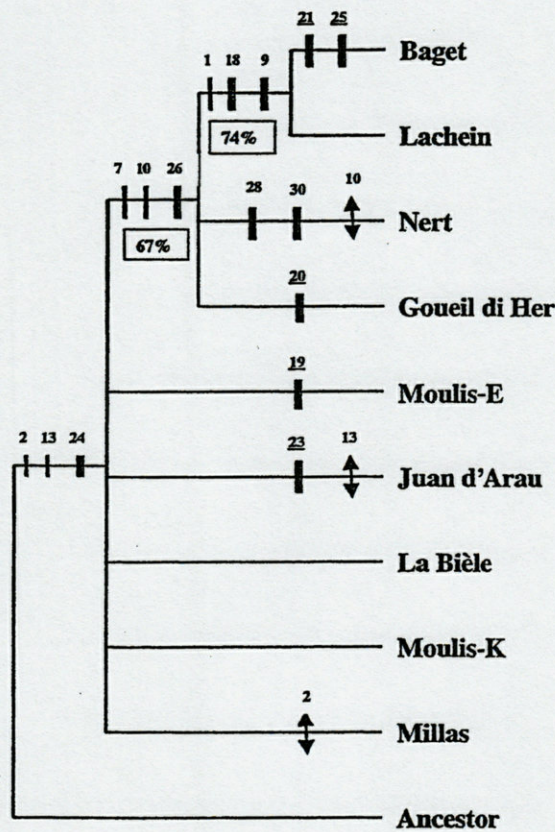
This is the correct Fig 6 which considers the numbers of the species mentioned in the Table I.

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Rappatoiolo Dossiccipol DL, Roush R & Defaeus A, 1993. Taxonomic diversity of groundwater Harpacticoida (Copepoda, Crustacea) in southern France. Vie Milieu 52(1):1-15.

This is the correct Fig 6 which correlates the numbers of the species mentioned in the Table1.

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TAXONOMIC DIVERSITY OF CRUSTACEA CYCLOPOIDA IN THE AUSTRIAN "DANUBE FLOODPLAIN" NATIONAL PARK

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CRUSTACEA, CYCLOPOIDA
HOTSPOT DIVERSITY SITE
TAXONOMIC DIVERSITY

ABSTRACT. – The groundwater dwelling cyclopoid assemblages of the "Danube Floodplain" National Park are more taxonomically diverse than earlier known for the regional cyclopoid fauna. Comparative studies on subsurface assemblages of two approximate 0.8 Km^2 areas in the National Park, the "Untere Lobau" and the "Regelsbrunner Au", show that the former site displays a higher taxonomic diversity than the latter, *i.e.*, higher values for the average taxonomic distinctness index (AvTD) and for the number of genera with reduced number of species (G$_{1/2}$ type). The conspicuous taxonomic diversity of the subsurface cyclopoids which exist in the "Untere Lobau" supports the characterization of this area as a hotspot of diversity. The hypogean fractions of cyclopoid assemblages of both the "Untere Lobau" and the "Regelsbrunner Au" areas display lower average taxonomic distinctness values than those of the entire assemblages from which they originate and higher variances of their taxonomic distinctness (VarTD). The species rich and taxonomically diverse cyclopoid fauna in the National Park confirm the high ecological and cultural value of this landscape and its importance with respect to Austrian interests in environmental protection of the natural heritage of the Danube.

CRUSTACEA, CYCLOPOIDA
SITES À DIVERSITÉ EXCEPTIONNELLE
DIVERSITÉ TAXONOMIQUE

RÉSUMÉ. – Les Cyclopoïdes peuplant le Parc National « Prairies du Danube » ont une diversité taxonomique importante par rapport à la faune régionale totale. L'étude comparative des communautés peuplant deux sites, "Untere Lobau" et "Regelsbrunner Au", d'une surface d'environ 0,8 Km^2 chacun, dans le Parc National, montre que le premier présente une diversité taxonomique importante: il se distingue par des valeurs élevées de l'index de la distinction taxonomique moyenne (average taxonomic distinctness – AvTD) ainsi que par le nombre des genres ayant un nombre réduit d'espèces (le type G$_{1/2}$). Le "Untere Lobau" est un site à diversité exceptionnelle (hotspot diversity site) tenant compte de la diversité taxonomique importante des Cyclopoïdes recensés dans les eaux souterraines de ce périmètre. La fraction hypogée des assemblages des Cyclopoïdes des deux sites, "Untere Lobau" et "Regelsbrunner Au", présentent des valeurs plus faibles pour l'indice de la distinction taxonomique moyenne et des valeurs plus importantes de la variance de la distinction taxonomique (Variance of taxonomic distinctness – VarTD), par rapport à celles de la communauté d'origine. La faune des Cyclopoïdes de ce Parc National, ayant une diversité taxonomique exceptionnelle, confirme l'intérêt écologique et culturel porté en Autriche pour la conservation de cette région naturelle du Danube.

INTRODUCTION

The present contribution examines the diversity of Cyclopoida, a microcrustacean group which commonly occurs in the alluvial plain of the Danube at Vienna and down this city in the "Danube Floodplain" National Park. In addition to species richness, our aim is to compare the taxonomic diversity of both epigean and hypogean dwelling taxa

of various assemblages occurring in subsurface aquatic habitats. Taxonomic diversity can be characterised in several ways, *e.g.*, through the examination of the distribution of taxa in an assemblage within a Linnaean classification system, or just by counting the number of taxa belonging to a given hierarchical level (*e.g.* number of species, of genera etc). Another approach is to use indices of diversity calculated from the presence/absence of taxa (*i.e.,* the average and variation of the taxo-

nomic distinctness of assemblages using the algorithms of Clarke & Warwick 1998, 2001). The information provided by the evaluation of the taxonomic diversity enables the characterization of hotspot diversity sites (Danielopol et al. 2002).

Analysis of the cyclopoid fauna of the "Danube Floodplain" National Park addresses the following questions:

(1) Is the taxonomic diversity of animal assemblages inhabiting subsurface areas higher or lower than those of epigean assemblages from the same area? (2) Can we characterise a hotspot diversity site using taxonomical diversity of Cyclopoida? This status for the subsurface part of the "Untere Lobau," an important part of the "Danube Floodplain" National Park, was proposed by Danielopol & Pospsisil (2001) using the entire list of stygobitic fauna of this area and by Danielopol et al. (2002) using the taxonomic diversity of crustacean Harpacticoida. (3) Which ecological factors play a role in the realisation of the observed cyclopoid diversity of the "Danube Floodplain" National Park? (4) Of what benefit is information on the taxonomic diversity of subterranean cyclopoids to the environmental planners and/or to the administration of the "Danube Floodplain" National Park?

Answers to these questions are needed because it was stressed that the diversity of stygobites expressed as species richness within local or regional areas is, in many cases, lower than the diversity of the epigean fauna (Marmonier et al. 1993, Sket 1999a). When integrated within the general discussion on the value of faunal protection, this latter opinion could give the impression that subterranean fauna plays a secondary role for decisions in environmental policies. To avoid such an interpretation when evaluating the diversity of cave fauna in the world, Culver & Sket (2000) proposed a simple rule of thumb in order to characterise hotspot diversity sites i.e., a minimum of 20 stygobitic species per cave site.

Rouch & Danielopol (1997) and Danielopol et al. (2000a) suggested that the aquatic subterranean fauna when examined in toto, i.e., both the hypogean and the epigean fractions, could be more diverse than commonly accepted. This impression emerges from various investigations, including ours, e.g., Lescher Moutoué (1973), Stoch (1987, 2001), Holsinger (1993), Reid (1993, 2001), Steenken (1998), Humphreys (1999), Strayer & Reid (1999), Sket (1999b), Danielopol et al. (1999, 2002), Dumas & Lescher-Moutoué (2001), Galassi (2001). In order to better evaluate the diversity of the world's subterranean fauna, several teams of specialists are involved in projects which aim to map taxonomic distributions at local, regional and continental scales, e.g., Gibert (2001), Stoch (2001), Christman & Culver (2001). The present study should be understood as a contribution to this international effort.

MATERIAL AND METHODS

Sampling sites: The "Danube Floodplain" National Park is a natural reserve of about 9300 hectares along the alluvial plain of the river. It is located in Vienna and east of Vienna and continues down to the Slovakian border (Fig. 1). The landscape of the park is remarkable
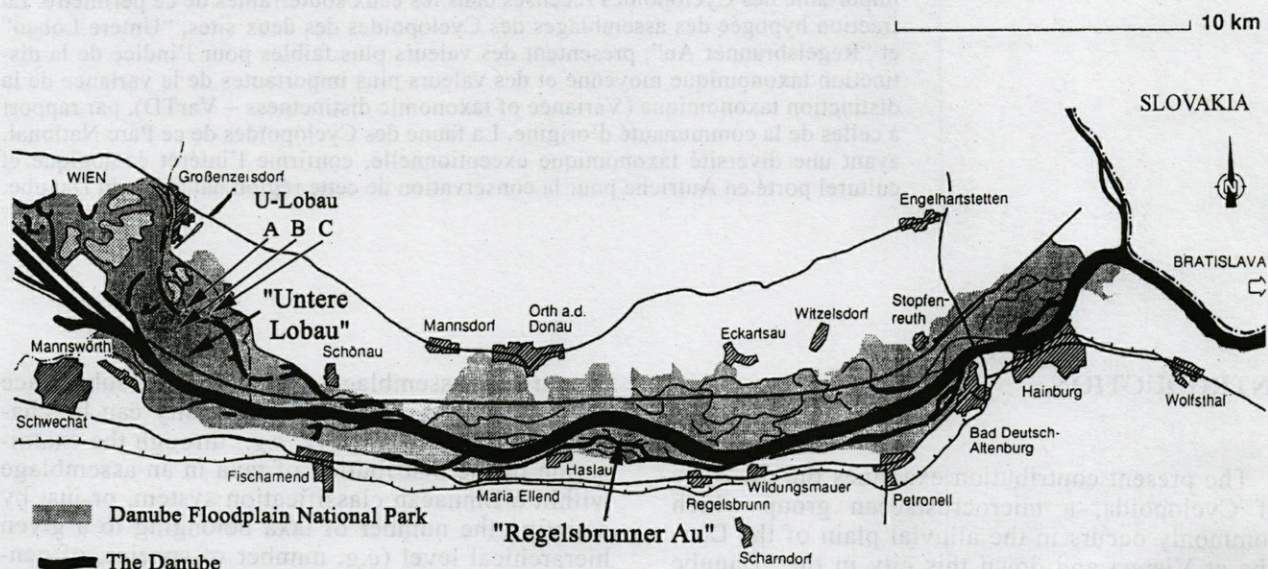

Fig. 1. – The "Danube Floodplain" National Park, with the location of the "Untere Lobau" and the "Regelsbrunner Au" areas and the U-Lobau ecosystems A, B and C (from Betriebsgesellschaft Marchfeldkanal 1994, modified).

through the diversity of terrestrial and aquatic ecosystems with a huge number of animal and vegetal species (Manzano 2000). The park's landscape is also highly appreciated for its tourist value and also it has been the object of various scientific research for many years, *e.g.,* Löffler (1976), Danielopol (1983), Danielopol *et al.* (2000b), Pospisil (1994a), Schiemer (1995), Tockner *et al.* (1999, 2000).

The "Untere Lobau" is an area along the Danube alluvial plain of about 10 Km length (Fig 1). The surface water systems are largely disconnected from the main channel of the Danube river. The subsurface of the alluvial plain in this area forms a large aquifer which is dynamically connected to the regional Marchfeld aquifer at the northern part and to the Danube river at the south-eastern part (Danielopol *et al.*, 2000b, 2001). Groundwater ecological investigations were carried out at three sites of the "Untere Lobau" (U-Lobau A, B, C, Fig. 1) within a perimeter of about 0.8 Km². The surface-water habitats of an old arm of the Danube, the Eberschüttwasser have also been included in various studies (Danielopol 1983, Pfaffenwimmer 1986, Pospisil 1999a). This backwater of the Danube connects the subsurface sites U-Lobau A and C (Danielopol 1983, Pospisil 1994b, Danielopol *et al.* 1997, 2000b, 2001). Epigean fauna of the Eberschüttwasser infiltrates into the surrounding groundwater habitats (see below).

The U-Lobau A site is an area of submerged alluvial sediment area of about 30 m² with a high permeability and a high rate of water infiltration; as an ecosystem it was thoroughly described by Danielopol (1983, 1989, 1991). The U-Lobau B is a large area of about 0.6 Km² located between the Eberschüttwasser and the Danube (for precise location and description see Pospisil 1994a, 1994b, 1999a and Danielopol *et al.* 2001). As an ecosystem, U-Lobau B displays the classic characteristics of the deep groundwater systems, *i.e.*, a very slow water velocity and low fluctuations of the temperature during the year; the fauna at this site mainly consists of exclusively hypogean dwelling animals, and it is seldom flooded by the Danube high waters. Finally, the U-Lobau C site displays characteristics intermediate of the other two Lobau sites. The water from Eberschüttwasser generally infiltrates into the aquifer, which has a surface area of about 900 m², and when the Danube and associated backwaters experience elevated discharge, this site is completely flooded. The subsurface fauna at the U-Lobau C site is composed of a mixture of epigean and hypogean animals with a predominance of epigean forms (Danielopol *et al.* 1992, 1994, 1997, 2000b).

The "Regelsbrunner Au" is a small floodplain (about 10 Km long) located about 25 Km east of Vienna (Fig. 1). The side arms were largely isolated from the Danube river but the hydrologic regime is much more active than those of the Lobau area previously discussed, especially during the high water levels of the river (Schiemer *et al.* 1999, Tockner *et al.* 1999, 2000). The sample sites used for groundwater research lay within a transect which crosses an area of about 0.8 Km². Three sites were chosen, each with piezometers located at 2-3 depths between 3 and 7 m deep. Two of the sites lay closely to the side arms while the third one is located outside the backwaters. Groundwater fauna was sampled every two months during 1994/1995 (leg I Wenzl) and 1997 (leg A Steininger).

The cyclopoid fauna: The cyclopoid data presented here stem from long-term investigations in two areas of the "Danube Floodplain" National Park: the "Untere Lobau" and the "Regelsbrunner Au" (Fig. 1). We used published data (Danielopol 1983, Pospisil 1994a, 1994b, 1999a, Danielopol *et al.* 1999a, 2001, Pospisil & Danielopol 2000, Danielopol & Pospisil 2001) as well as unpublished information with the kind permission of several students from the Limnological Department, University of Vienna: G Pfaffenwimmer (doctoral thesis 1986), T Hein, A Steininger and I Wenzl (sampling protocols and material offered to taxonomic identification). The subterranean cyclopoid fauna sampled in the "Regelsbrunner Au" by I Wenzl and A Steininger were identified by one of us (PP) and presented in Pospisil & Danielopol (2000).

In order to better characterise the regional diversity of the cyclopoid fauna occurring in Lower Austria around the "Danube Floodplain" National Park, we also used information existing in Humpesch & Moog (1994), Gaviria (1998a, 1998b), Schönbauer (1999), Tockner *et al.* (2000), Baranyi *et al.* (2002).

Analytical methods: The taxonomic diversity of the cyclopoid assemblages were characterised with different descriptors following the protocols used in Rouch & Danielopol (1997) and (Danielopol *et al.* 2002): (1) the taxonomic list of the assemblage, including three levels of the Linnaean hierarchy: the species, the genus and the subfamily; (2) the species richness, the number of epigean and hypogean taxa; (3) the higher-taxon richness, represented by the number of genera with few and with many species, the so-called $G_{1/2}$ and G_3 taxa (Danielopol *et al.* 2002); (4) the average of taxonomic distinctness (AvTD = Delta+) and the variation of taxonomic distinctness (VarTD = Λ +) as described by Clarke & Warwick (1998, 1999, 2001). These two latter indices are especially well suited for the characterisation of the taxonomic diversity of groundwater dwelling crustaceans (Danielopol *et al.* 2002) because they are independent of sampling effort, thus allowing comparisons between present/absent species in the assemblages (Warwick & Clarke 2001). Moreover we will compare the taxonomic distinctness of a local assemblage with those of the total species list of a regional assemblage following the randomisation test and the 95% probability funnel method of Clarke & Warwick (1998) using 5000 random selections from the master list of 38 species. This procedure allowed us to verify if the observed data depart significantly from sub-samples with an equivalent number of species extracted randomly from the total (regional) species list.

The values of the indices for taxonomic distinctness (AvTD and VarTD) as well as the Clarke & Warwick randomisation test were computed with the computer package PRIMER-5 (Plymouth Routines in Multivariate Ecologic Research) for Windows, version 5.2 (Clarke & Gorley 2001).

RESULTS

The number of cyclopoid species in the National Park at the two sites, the "Untere Lobau" and the

Table I. – The taxonomic list of the Cyclopoida sampled in the "Danube Floodplain" National Park, the "Untere Lobau" (U-Lobau) and the "Regelsbrunner Au" areas: S1 – U-Lobau A; S2 – U-Lobau B; S3 – U-Lobau C; S4 – Regelsbrunner Au; S5 – Eberschüttwasser; S1 – S4, subsurface habitats, S5, surface benthic habitat; S1, S5 – cyclopoids det. by G Pfaffenwimmer and P Pospisil; S2 – S4, cyclopoids det. P Pospisil; EC – Ecological characterisation; Hy – Hypogean (= stygobitic) taxon; Ep – Epigean taxon; Cy – Cyclopoida. * Species identified by G Pfaffenwimmer in Danielopol 1983.

No.	EC	TAXA	S1	S2	S3	S4	S5
		Fam. Cyclopidae Sars					
		S-Fam. Eucyclopinae Kiefer					
1	Hy	Austriocyclops vindobonae Kiefer	-	+	-	-	-
2	Ep	Eucyclops serrulatus (Fischer)	+	-	+	-	+
3	Ep	Eucyclops speratus (Lilljeborg)	-	-	-	+	-
4	Hy	Eucyclops graeteri Kiefer	+	-	+	+	-
5	Ep	Eucyclops sp.	-	-	+	-	-
6	Ep	Macrocyclops albidus (Jurine)	-	-	+	-	+
7	Ep	Macrocyclops fuscus (Jurine)	-	-	-	-	+
8	Ep	Paracyclops fimbriatus (Fischer)	-	-	+	-	+
9	Ep	Paracyclops sp.	-	-	+	-	-
		S-Fam. Cyclopinae (Dana) Kiefer					
10	Ep	Cyclops vicinus Fischer	-	-	-	-	+
11	Ep	Cyclops strenuus Fischer	-	-	-	-	+
12	Ep	Cyclops sp.	-	-	+	-	-
13	Hy	Acanthocyclops rhenanus Kiefer*	+	-	+	-	-
14	Hy	Acanthocyclops gmeineri Pospisil	-	+	-	+	-
15	Hy	Acanthocyclops kieferi (Chappuis)	+	+	-	-	-
16	Ep	Acanthocyclops vernalis (Fischer)	-	-	+	-	+
17	Hy	Acanthocyclops venustus ssp.(Norman & Scott)	+	+	+	+	-
18	Hy	Acanthocyclops sensitivus (Graeter & Chappuis)	+	+	+	+	-
19	Ep	Acanthocyclops viridis (Jurine)	-	-	+	-	-
20	Ep	Acanthocyclops robustus (Sars)	+	-	+	+	+
21	Ep	Acanthocyclops sp.	+	-	-	-	-
22	Hy	Diacyclops cohabitatus Monchenko	-	-	+	-	-
23	Ep	Diacyclops bicuspidatus (Claus)	-	-	-	-	+
24	Hy	Diacyclops danielopoli Pospisil & Stoch	-	+	-	+	-
25	Ep	Diacyclops disjunctus (Thallwitz)	-	-	+	-	-
26	Ep	Diacyclops languidoides (Lilljeborg)	-	-	+	-	-
27	Hy	Diacyclops felix Pospisil & Stoch	+	+	+	+	-
28	Ep	Diacyclops languidus (Sars)	-	-	+	-	-
29	Ep	Cryptocyclops bicolor (Sars)	-	-	+	-	-
30	Hy	Graeteriella unisetigera (Graeter)	-	+	-	+	-
31	Ep	Thermocyclops crassus (Fischer)	-	-	+	-	+
32	Ep	Thermocyclops oithonoides (Sars)	-	-	+	-	+
33	Ep	Thermocyclops sp.	-	-	-	-	+
34	Ep	Megacyclops viridis (Haller)	-	-	-	-	+
35	Ep	Mesocyclops leuckarti (Claus)	-	-	+	-	+
36	Ep	Metacyclops planus (Gurney)	-	-	+	-	-
37	Ep	Microcyclops varicans (Sars)	-	-	+	-	-
38	Ep	Microcyclops rubellus (Lilljeborg)	-	-	-	-	+
Total Cy		Species / Site	16	9	18	11	16
Total Hy		Species / Site	4	8	4	8	0

"Regelsbrunner Au" is 38 (Table I), of which four species were left in open nomenclature. All these species belong to the family Cyclopidae Sars and are distributed within two subfamilies, the subfamily Eucyclopinae Kiefer, represented by 9 species, and the subfamily Cyclopinae (Dana) Kiefer, with 29 species. There are 27 epigean and 11 stygobitic species.

Of the five sites we investigated (Table I), the most species rich is the site U-Lobau C with 18 species (14 epigean and 4 hypogean taxa), followed by the surface water habitats of the backwater Eberschüttwasser (16 epigean species) and the subsurface site U-Lobau A (12 epigean and 4 hypogean species). In the 0.8 Km² "Untere

Lobau" area (Tables I II, S1–S3, U-Lobau A+B+C) we identified 30 species, of which 10 are stygobites). The sites "Regelsbrunner Au" (S4) and U-Lobau B (S2) display lower species richness (11 and 9 species respectively, of which 8 are stygobites). The total number of $G_{1/2}$ and G_3 genera within the two areas we investigated (Table II) is high (9 and 5, respectively) whereas, the number of $G_{1/2}$ and G_3 genera (Table II) of most of the Lobau and Regelsbrunn wetland subsurface sites, is reduced (2 – 4 $G_{1/2}$, respectively 1 – 2 G_3 genera per site). This result was obtained from analyses including both epigean and hypogean genera, and also from analyses of sytgobitic genera only. The backwater Eberschüttwasser (S5) and the subsurface U-Lobau C site (S3) have a high num-

Table II. – Diversity of Cyclopoida within the "Danube Floodplain" National Park; $G_{1/2}$ – genus with 1 or 2 species; G_3 – genus with 3 or more species; AvTD – Average taxonomic distinctness; VarTD – Variation of taxonomic distinctness; Hy – stygobitic fraction of taxa (additional explanations in text and Table I).

No.	Sites within the Danube area	Assemblage Code	Species Richness (No.)	Hypogean Species (No.)	Genus $G_{1/2}$ (No.)	Genus G_3 (No.)	AvTD	VarTD
0	"Danube Floodplain" National Park	DFP	38	11	9	5	75.63	446
1	Eberschüttwasser	E	16	0	9	1	75.56	346.9
2	U-Lobau/A+B+C	LABC	30	10	10	3	74.87	481.9
3	U-Lobau/A+B+C-Hy	LABCHy	10	10	3	2	71.85	590
4	U-Lobau/A	LA	16	4	4	2	73.61	609.2
5	U-Lobau B	LB	9	8	2	2	71.3	688.4
6	U-Lobau/B-Hy	LBHy	8	8	2	2	73.81	663.3
7	U-Lobau/C	LC	18	4	9	2	70.15	336.4
8	Regelsbrunner Au	R	11	8	2	2	69.09	640.6
9	Regelsbrunner Au-Hy	RHy	8	8	1	2	64.29	629.3

ber of $G_{1/2}$ genera (9) and a low number of G_3 genera (1-2), while the entire subsurface Lobau area (U-Lobau/A+B+C, Table II) is characterised by 10 $G_{1/2}$ genera and only 3 G_3 genera.

The two cumulated areas we investigated had the highest value of average taxonomic diversity (75.63) in the National Park (Table II). The AvTD value was high for the epigean assemblage of the backwater Eberschüttwasser (75.56), while the values for the subsurface assemblages are lower, *i.e.*, U-Lobau/ A+B+C area, 74.87, the U-Lobau A site, 73.61 and the site U-Lobau B, 71.3. The AvTD values for the stygobitic fractions of the U-Lobau B and the U-Lobau/A+B+C lay in between the previous data (73.81 and 71.85). The AvTD values are even lower for the subsurface cyclopoid fauna of the "Regelsbrunner Au" area: 69.09 for the entire assemblage and only 64.29 for the exclusively hypogean fraction.

The variations in taxonomic distinctness (Table II) were low (between 336.4 and 481.9) for assemblages or species collections from both surface and subsurface areas which had a high number of $G_{1/2}$ genera (9–10) *i.e.*, those of the Eberschüttwasser, the U-Lobau A+B+C and the U-Lobau/C assemblages. High values (between 590 and 688.4) were observed for those assemblages with low number of $G_{1/2}$ genera (1–3), *i.e.*, the assemblages of the "Regelsbrunner Au", of the U-Lobau A and the hypogean fractions of the U-Lobau/A+B+C and U-Lobau/B.

The AvTD values for the 9 assemblages investigated (Table II) lay inside the 95% confidence funnel (Fig. 2) calculated from the total species list of Table I.

DISCUSSION

From the information published by Gaviria (1998a), Pospisil & Stoch (1999), Stoch & Pospisil
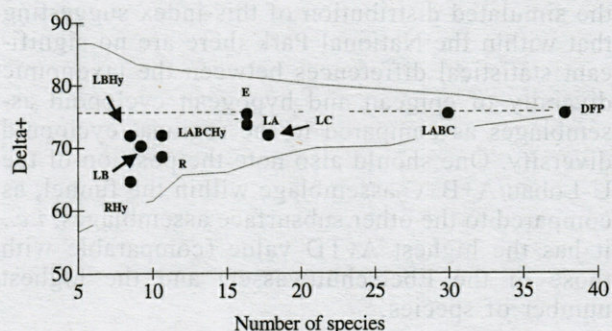
Fig.2. – Average taxonomic distinctness values (Delta+) for nine cyclopoid assemblages from the "Danube Floodplain" National Park, plotted against the observed number of species for the total list of the "Untere Lobau" and the "Regelsbrunner Au" areas (DFP). Dashed line, the simulated mean; thin line, the 95% probability funnel for the expected range of Delta+ values constructed from random sublists of species. Assemblage codes as in Table II.

(2000a, 2000b) the number of recorded cyclopoid species in Austria is 54; they belong to one family, the Cyclopidae, and are classified in 18 genera and 2 sub-families. The cyclopoid fauna recorded in the "Danube Floodplain" National Park is formed by the 34 species discussed here and three species, *Ectocyclops phaleratus* (Koch), *Diacyclops crassicaudis* (Sars) and *Diacyclops bisetosus* (Rehberg), mentioned by Gaviria (1998a) as occurring in the Lobau but *de facto* sampled outside this area by one of us (PP), at Eckartsau. The number of cyclopoid species occurring in the "Danube Floodplain" National Park (without the four species left in open nomenclature) represents 68% of the present known Austrian fauna. The species richness of the regional cyclopoid fauna of the Danube area within the Vienna Basin is 44 (Kiefer 1964, Gaviria 1998a, 1998b, Schönbauer 1999, Pospisil & Danielopol 2000), hence only few species were not yet recorded in the "Danube

Floodplain" National Park like the stygobitic cyclopoid *Paragraeteriella* sp., known from the deeper part of the Marchfeld aquifer (Pospisil & Danielopol 2000), *Cyclops insignis* Claus found in the Danube River, at Freudenau (Schönbauer 1999), *Paracyclops poppei* (Rehberg) sampled in the new built Marchfeld Canal (Gaviria 1998b), *Megacyclops gigas* Claus, *Paracyclops affinis* (Sars), *Eucyclops macrurus* (Sars), *E. macruroides* (Lilljeborg) observed in the "Alte Donau" in Vienna (Gaviria 1998a). The taxonomic diversity expressed as number of genera, in the area investigated by us, represents 87.5% of the regional generic taxa.

When characterised by the AvTD index the taxonomic diversities of subsurface cyclopoid assemblages fall within the 95% probability funnel for the simulated distribution of this index suggesting that within the National Park there are no significant statistical differences between the taxonomic diversity of epigean and hypogean cyclopoid assemblages as compared to the regional cyclopoid diversity. One should also note the position of the U-Lobau/A+B+C assemblage within the funnel, as compared to the other subsurface assemblages, *i.e.,* it has the highest AvTD value (comparable with those of the Eberschüttwasser) and the highest number of species.

The high values of the VarTD for the hypogean fractions of cyclopoid assemblages reflects an interesting characteristic of their taxonomic diversity, *i.e.,* the contrasting stygobitic lineages: on one side the specious G_3 genera *Acanthocyclops*, and *Diacyclops* on the other side, the existence of lineages with rare species which belong to $G_{1/2}$ genera. The protection of these latter lineages against extinction is especially imperative. This situation should be compared with that of the surface cyclopoid fauna of the backwater Eberschüttwasser which has a more even taxonomic distribution and, hence, was assigned a lower VarTD value. This site has a high number of $G_{1/2}$ genera with generalist species, for which special protection measures are not required.

The cyclopoid assemblage of the Eberschüttwasser has a higher species richness and generic taxonomic diversity in comparison to those recorded in the impounded sectors of the Danube river. In the Freudenau area 11 species belonging to six genera (4 $G_{1/2}$ and 2 G_3 taxa) and 2 subfamilies were identified (Schönbauer 1999), while in the Altenwörth impoundment 10 species, belonging to eight $G_{1/2}$ genera and two subfamilies were sampled (A Herzig, pers comm to DLD).

Because of its subsurface cyclopoid fauna with high species richness, high taxonomic diversity and high number of stygobitic species, the "Untere Lobau" area should be considered a hotspot diversity site. This decision confirms the previous esti-

mation of the site's unusually rich diversity, evaluated with other animal groups (Danielopol & Pospisil 2001, Danielopol *et al.* 2002). The taxonomic diversity of the subsurface cyclopoid fauna of the Lobau is comparable with those of another hotspot diversity area, the system Postojna-Planina cave system, where Brancelj (1987) mentioned 24 cyclopoid species (6 stygobites) belonging to 11 genera (8 $G_{1/2}$, 3 G_3 taxa) and two subfamilies.

The stygobitic fraction of the cyclopoid assemblages of the "Untere Lobau" and the "Regelsbrunner Au" areas, with lower taxonomic diversity values than those of the entire assemblage from which they originate, confirm the opinions of Marmonier *et al.* (1993) and Sket (1999a) mentioned above (*cf.* Introduction), that the faunas dominated by stygobitic taxa are less diverse than the epigean assemblages.

The taxonomic diversity values of subsurface dwelling cyclopoid assemblages of the two investigated areas, the "Untere Lobau" and the "Regelsbrunner Au", are in our opinion related to the structure and functioning of the landscape ecosystems to whom they belong. The "Untere Lobau" area is characterised by surface aquatic systems (*e.g.,* the Eberschüttwasser) which do not depend strongly on the hydrological dynamics of the Danube river (Schiemer 1999, Tockner *et al.* 2000, Pospisil 1999a, Danielopol *et al.* 2000b, 2001).

The aquatic landscape in the Danube wetlands of the National Park is formed by a mosaic of ecosystems, tightly interconnected. One notices the strong connectivity between the epigean Eberschüttwasser system with the subsurface U-Lobau ecosystems (especially the A and C ones) as described in Danielopol *et al.* 1997, 2000b, 2001). This explains the high number of epigean species which colonises the subsurface habitats of this area. In contrast, the dynamics of the U-Lobau B system, which is mainly recharged by the Danube river is much slower than those of the U-Lobau A and C ecosystems (Danielopol *et al.* 2000b, 2001). The number of epigean species which could be introduced from the Danube river is low; it reflects the general low diversity of the cyclopoid fauna in the main channel of the river. For instance, for the whole Austrian sector Humpesch & Moog (1994) could mention only 12 species belonging to eight genera (7 $G_{1/2}$ 1 G_3 taxa) and two subfamilies.

The aquatic system of the "Regelsbruner Au" area is much more strongly dependent on the hydrological dynamics of the Danube (Schiemer *et al.* 1999, Ward *et al.* 1999, Tockner *et al.* 2000, Schiemer 2001). The cyclopoid fauna of the epigean aquatic systems is less diverse than that of the Eberschüttwasser. During the one year sampling program, when the subsurface cyclopoids mentioned here were sampled (A Steininger unpubl.), only six species belonging to five $G_{1/2}$

genera were recorded in the surface backwaters (Tockner et al. 2000, T Hein, pers comm to DLD). Increased connectivity between the Danube river and the Regelsbrunner-floodplain area leads to strong flushing effects of the epigean cyclopoid fauna during high water levels (Baranyi et al. 2002). Hence the magnitude of the epigean fraction which are able to colonise the aquatic subsurface habitats in the Regelsbrunner area is reduced. Additionally, because gravel sediments become densely packed in this area and/or soft sediment accumulates, the infiltration of surface water into the Regelsbrunner aquifer along the side arms is probably more reduced than at the sites U-Lobau A and C. Therefore the taxonomic diversity of the former area is lower because of the few epigean cyclopoid species and a higher number of hypogean taxa belonging to few genera. In this way the cyclopoid fauna of the "Regelsbrunner Au" more closely resembles the assemblage of the U-Lobau B than the other Lobau cyclopoid assemblages.

The aim of the "Danube Floodplain" National Park is to protect one of the most diverse areas of Central Europe; about 700 species of plants and over 300 animal species exist (Manzano 2000, Tockner et al. 2000). Considerations of aquatic animal diversity, often emphasize fishes rather than invertebrate fauna (Schiemer & Waidbacher 1992, Schiemer 1999, Ward et al. 1999, Tockner et al. 2000). Our study of cyclopoid crustaceans presents data supporting their inclusion as a focal group on faunal diversity lists; they are very well suited to characterise locations of high diversity.

Besides ensuring environmental protection, the administrators of this National Park should recognise the existence of rare species in the Danube wetland landscape which have to be better ecologically studied in order to be protected. Pospisil & Danielopol (1990) proposed that the administration of the Danube National Park include groundwater ecology subject matter in their scientific programs. This aim was partly fulfilled through a series of long-term ecological projects done by various interdisciplinary research groups in both the "Untere Lobau" and the "Regelsbrunner Au" areas (cf. Material & Methods section). Here we want to point out that future scientific activities should also include ecological studies on rare stygobitic cyclopoid species like Austriocyclops vindobonae, Graeteriella unisetigera, Acanthocyclops sensitivus, Acanthocyclops gmeineri, Diacyclops disjunctus, Diacyclops cohabitatus etc, species that were difficult to locate and further to sample outside the National Park (Pospisil & Stoch 1997, Pospisil 1989, 1999b, Stoch & Pospisil 2000a, 2000b, Pospsil & Danielopol 2000, Danielopol et al. 2001). Such activities are not only of scientific interest but also represent a cultural contribution in that ecological information can further be disseminated to citizens interested in the maintenance of nature's splendour

(for similar arguments see also Danielopol 1989, Pospisil & Danielopol 1990, Marmonier et al. 1997, Danielopol & Pospisil 2001).

CONCLUSIONS

1. The "Danube Floodplain" National Park has a very species rich and taxonomically diverse cyclopoid fauna, when compared to the regional cyclopoid fauna or to the entire Austrian records.
2. The taxonomic diversity values of subsurface dwelling cyclopoid assemblages differ from site to site depending on the position of these sites within the landscape ecosystems.
3. Some of subsurface cyclopoid assemblages display values of taxonomic diversities similar to those of surface-water systems.
4. The hypogean fractions of species rich cyclopoid assemblages display lower taxonomic diversity values than those of the entire assemblage from which they originate.
5. The "Untere Lobau" area we investigated, taking in consideration the subsurface cyclopoid fauna with its high species richness, high taxonomic diversity and high number of stygobitic species, should be considered a hotspot diversity site.
6. The species rich and taxonomically diverse cyclopoid fauna documented in the "Danube Floodplain" National Park are good arguments for further protecting this unique natural landscape and for further funding projects dealing with groundwater ecology topics.

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DISCRIMINATIVE VALUE OF THE MERISTIC CHARACTERS OF *ATHERINA BOYERI*, LAGOON POPULATIONS

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ATHERINA BOYERI
MEDITERRANEAN LAGOONS
MERISTIC CHARACTERS

ABSTRACT. – The statistical analyses of nine meristic characters of *Atherina boyeri*, collected in Mediterranean lagoon waters, show the homogeneity of the French populations and the heterogeneity of those of the Tunisian lagoons. Of the set of characters taken into account, only the numbers of longitudinal line scales (SC), vertebrae (VE) and pectoral fin rays (PE) support a clear divergence between the individuals of the European and Tunisian lagoons. For these three characters, the group of the Lion gulf and Corsica populations is characterized by higher mean values than those observed in the Tunisian lagoons.

ATHERINA BOYERI
LAGUNES MÉDITERRANÉENNES
CARACTÈRES MÉRISTIQUES

RÉSUMÉ. – Les analyses statistiques de 9 caractères méristiques de *Atherina boyeri*, collectée dans les eaux lagunaires de Méditerranée, montrent l'homogénéité des populations françaises et l'hétérogénéité de celles des lagunes tunisiennes. Sur l'ensemble des caractères pris en compte, seul le nombre d'écailles en ligne longitudinale (EC), de vertèbres (VE) et de rayons des nageoires pectorales (PE) indique l'existence d'une nette divergence entre les individus des lagunes européennes et tunisiennes. Pour ces trois caractères, le groupe des populations du golfe du Lion et de Corse se caractérise par des valeurs moyennes plus élevées que celles observées dans les lagunes tunisiennes.

INTRODUCTION

Sand smelts, *Atherina boyeri* Risso, 1810 of Tunisian and French lagoons were the object of studies on the meristic characters (Kiener & Spillmann 1969, Marfin 1982, Trabelsi & Kartas 1985, Trabelsi 1989, Kartas & Trabelsi 1990). These studies permitted to characterize the different populations occupying these environments. Nevertheless, these works had a limited extent because the results obtained are not easily comparable (the respective characters differ according to authors, strengths of the French populations are very weak and the ways of counting were not defined). The aim of our survey is to establish, while homogenizing strenghts and processes of sampling and analysis, whether populations occupying lagoons of dif-

ferent geographical positions and environmental conditions are dissimilar or whether they constitute a homogeneous whole.

MATERIALS AND METHODS

A. boyeri (Fig. 1) individuals were collected, by means of capetchads, in seven Mediterranean lagoons (Fig. 2). They originate from the Lion gulf (Thau (T), Mauguio (G), Camargue (C)), Corsica (Biguglia (B)) and Tunisia (Tunis (U), Bizerta (D), Ichkeul (E)). All fishes were preserved in 10% formalin. For each individual, the number of dorsal (D1, D2), anal (AN) and pectoral (PE) fin rays, of longitudinal line scales (SC), vertebrae (VE) and of gillrakers on the first left bran-
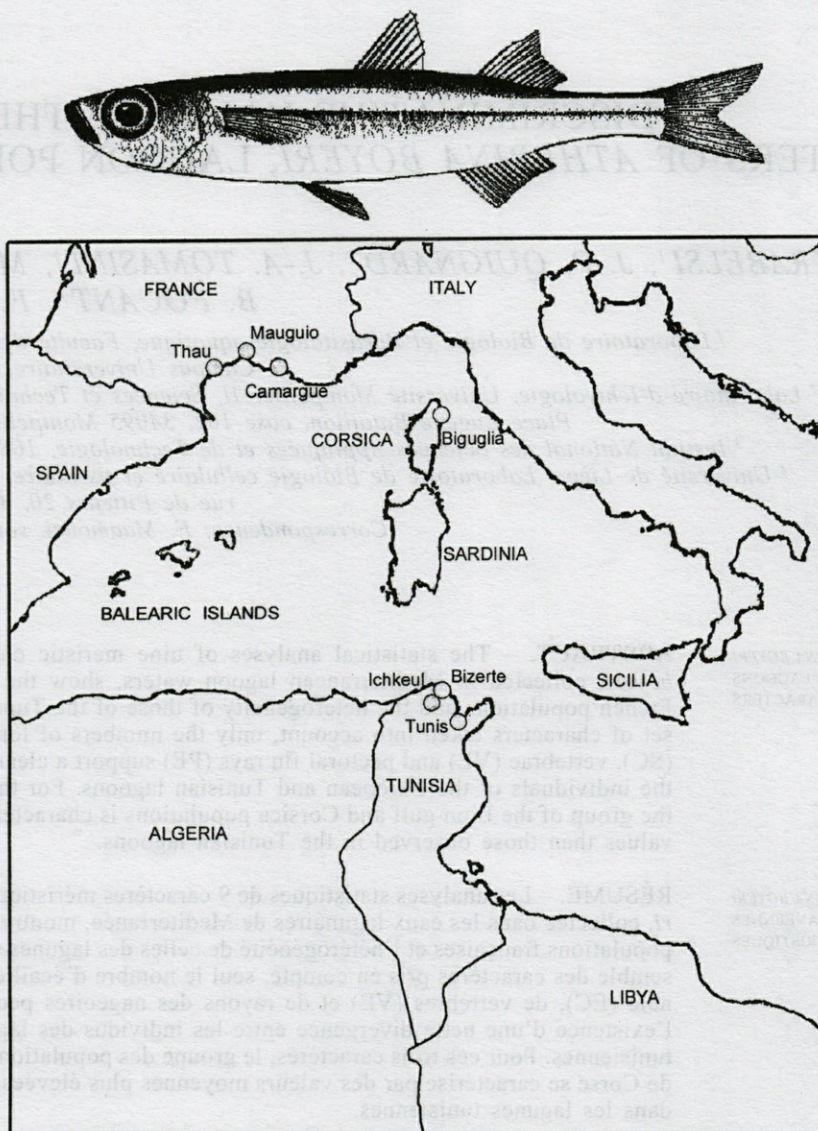
Fig. 1. – Top, *Atherina boyeri* Risso, 1810. Bottom, Geographical distribution of the different lagoons.

chial arc (upper (UG), lower (LG) and total (TG) gillrakers) were recorded.

Comparisons of mean values, variances, standard deviations between the various lagoonal populations of *A. boyeri* were carried out by means of Student "t", Fisher "F", Mayr-Linsley-Usinger "C.D." and Duncan "D" tests (Fisher 1936, Gery 1962, Dagnelie 1975). These tests permit the statistical evaluation of similarities or differences, for a given character, between the samples taken two by two.

In order to obtain a better estimation of divergences between the samples, a multidimensional analysis was made covering simultaneously all the characters and the analysed samples. The canonical discriminative analysis allows to discriminate, at best, the samples of the same species or of different ones (Fisher 1936, Dagnelie 1975, Semple *et al.* 1991). It leads to a graphical representation of the distribution of the different samples in a defi-

ned plane by the various canonical components taken two by two (SAS 1990). This procedure also provides phenotypical distances (D2=Mahalanobis distances). The computation of Mahalanobis distances allows to obtain a graphical representation (Mahalanobis dendrogram) of samples in a P dimension space (P is the number of studied characters).

RESULTS

Vertebrae (VE)

For this parameter, a latitudinal decrease of the mean value is observed from the north to the south. Within this cline, a clear difference between the

Table I. – Mean comparison by the Duncan test. The populations surrounded by a line form a group the means of which are significantly similar. The populations not connected by a line have significantly different means. Meristic character: VE: Vertebrae, SC: Longitudinal Line Scales, UG: Upper Gillrakers, LG: Lower Gillrakers, TG: Total Gillrakers, PE: number of the pectoral fins rays, D1: number of the first dorsal fin rays, D2: number of the second dorsal fin rays and AN: number of the anal fin rays. min=minimum, max=maximum, x=mean, s=standard deviation.

VE		Camargue	Mauguio	Thau	Biguglia	Ichkeul	Bizerta	Tunis
	min-max	42 _ 47	43 _ 46	43 _ 47	43 _ 46	42 _ 45	40 _ 45	39 _ 43
	x	44.53	44.51	44.51	44.49	43.1	42.15	41.34
	s	0.87	0.798	0.859	0.659	0.81	1.077	0.89

SC		Camargue	Biguglia	Mauguio	Thau	Ichkeul	Bizerta	Tunis
	min-max	44 _ 48	43 _ 48	44 _ 47	44 _ 47	41 _ 46	40 _ 45	39 _ 43
	x	45.4	45.39	45.35	45.33	43.23	42.08	41.21
	s	0.876	0.898	0.857	0.9	0.941	1.041	1.028

UG		Bizerta	Tunis	Thau	Mauguio	Ichkeul	Biguglia	Camargue
	min-max	7 _ 8	7 _ 9	6 _ 8	6 _ 9	6 _ 8	6 _ 8	6 _ 8
	x	7.59	7.46	7.36	7.31	7.24	7.16	7.12
	s	0.494	0.54	0.503	0.526	0.534	0.465	0.456

LG		Bizerta	Tunis	Camargue	Mauguio	Thau	Ichkeul	Biguglia
	min-max	18 _ 22	18 _ 21	17 _ 20	16 _ 21	17 _ 21	17 _ 21	17 _ 21
	x	19.71	19.43	19.02	19.02	18.73	18.61	18.51
	s	0.808	0.844	0.752	0.921	0.763	0.886	0.937

TG		Bizerta	Tunis	Mauguio	Camargue	Thau	Ichkeul	Biguglia
	min-max	25 _ 30	25 _ 30	23 _ 29	23 _ 28	24 _ 29	24 _ 29	23 _ 29
	x	27.3	26.89	26.33	26.14	26.09	25.85	25.67
	s	1.03	1.188	1.215	1.015	1.026	1.209	1.19

PE		Camargue	Thau	Mauguio	Biguglia	Ichkeul	Bizerta	Tunis
	min-max	12 _ 16	13 _ 16	13 _ 16	13 _ 16	13 _ 15	12 _ 15	12 _ 15
	x	14.47	14.21	14.18	14.1	13.72	13.37	13.02
	s	0.688	0.656	0.657	0.674	0.653	0.63	0.586

D1		Mauguio	Thau	Ichkeul	Biguglia	Camargue	Bizerta	Tunis
	min-max	6 _ 9	6 _ 9	6 _ 10	6 _ 10	6 _ 9	6 _ 10	5 _ 9
	x	7.79	7.78	7.59	7.52	7.49	7.48	7.02
	s	0.671	0.719	0.842	0.731	0.643	0.87	0.71

D2		Ichkeul	Bizerta	Biguglia	Camargue	Thau	Tunis	Mauguio
	min-max	10 _ 14	10 _ 14	10 _ 14	10 _ 13	9 _ 13	10 _ 14	9 _ 13
	x	11.67	11.38	11.35	11.35	11.3	11.27	11.23
	s	0.779	0.722	0.672	0.716	0.704	0.694	0.694

AN		Camargue	Ichkeul	Bizerta	Tunis	Thau	Biguglia	Mauguio
	min-max	11 _ 16	12 _ 16	12 _ 16	11 _ 16	11 _ 15	11 _ 15	12 _ 15
	x	13.49	13.45	13.41	13.41	13.38	13.23	13.14
	s	0.937	0.857	0.793	0.889	0.85	0.827	0.752

Tunisian and French lagoon sand smelts is observed. The latter form a homogeneous group having a vertebral mean of 44.5; a mode of 45 and individual values ranging from 42 to 47. The three Tunisian populations differ among themselves in their means, modes and extreme values which are lower than those characterizing the French populations (Tables I, II).

Longitudinal line scales (SC)

The analysis of this character leads to the same conclusions as those acquired with the vertebrae numbers. The French lagoon populations form a homogeneous group characterized by a mean (45.4), a mode (45) and a maximum value (48) higher than those observed in the Tunisian lagoons which are statistically different between themselves (Tables I, III).

Gillrakers (UG, LG, TG)

The numbers of upper (UG), lower (LG) and total (TG) gillrakers do not show any correlation with the fish length, which has permitted the calculation and multiple mean comparison between the different populations. The mean numbers fluctuate between 7 and 8 upper gillrakers, 18 and 20 lower gillrakers, 25 and 28 total gillrakers.

– The LG character seems to be most discriminative, it permits the distinction of four groups (Bizerta / Tunis / Camargue-Mauguio / Thau-Ichkeul-Biguglia) (Tables I, IV).

– TG comes in the second place (formation of three groups: Bizerta / Tunis / Mauguio-Camargue -Thau-Ichkeul-Biguglia) (Tables I, V).

– UG does not permit any discrimination between the different studied populations (recognition of only one group) (Tables I, VI).

Table II, on the left. – Number of vertebrae in different lagoon populations. Table III, on the right. – Number of longitudinal line scales in different lagoon populations. Top: Statistical parameters. Middle: Tests of Student "t" on means and Fisher "F" on variances. Bottom, Divergence coefficient "C.D." on means and standard deviations.

Table II – Vertebrae

Vertebrae	38	39	40	41	42	43	44	45	46	47	n	x	s	s2
Thau						13	33	45	8	1	100	44,510	0,859	0,737
Mauguio						10	38	43	9		100	44,510	0,798	0,636
Camargue				2		6	41	40	10	1	100	44,530	0,870	0,757
Biguglia						4	48	43	5		100	44,490	0,659	0,434
Ichkeul					6	81	142	84	13		326	43,052	0,859	0,739
Bizerta		4	23	41	20	10	2				100	42,150	1,077	1,159
Tunis	3	10	60	228	156	23					480	41,235	0,853	0,727

F \ t	Thau	Mauguio	Camargue	Biguglia	Ichkeul	Bizerta	Tunis
Thau	—	0,000	0,164	0,185	14,852 ++	17,139 ++	34,745 ++
Mauguio	1,159	—	0,170	0,193	15,697 ++	17,614 ++	36,906 ++
Camargue	1,027	1,190	—	0,367	14,902 ++	17,194 ++	34,570 ++
Biguglia	1,698 ++	1,465 +	1,744 ++	—	17,691 ++	18,539 ++	42,541 ++
Ichkeul	1,002	1,162	1,025	1,702 ++	—	7,663 ++	29,552 ++
Bizerta	1,573 +	1,822 ++	1,531	2,671 ++	1,569	—	7,993 ++
Tunis	1,014	1,143	1,041	1,675 ++	1,016	1,594 ++	—

C.D.	Mauguio	Camargue	Biguglia	Ichkeul	Bizerta	Tunis
Thau	0,000	0,012	0,013	0,849	1,219 +	1,913 ++
Mauguio		0,012	0,014	0,880	1,259 +	1,984 ++
Camargue			0,026	0,855 +	1,223 +	1,912 ++
Biguglia				0,947 +	1,348 +	2,153 ++
Ichkeul					0,466	1,061 +
Bizerta						0,474

Table III – Scales

Scales	39	40	41	42	43	44	45	46	47	48	n	x	s	s2
Thau						21	33	38	8		100	45,330	0,900	0,809
Mauguio						15	45	30	10		100	45,350	0,857	0,735
Camargue						15	40	36	8	1	100	45,400	0,876	0,768
Biguglia					1	13	43	33	9	1	100	45,390	0,898	0,806
Ichkeul					7	54	119	74	24	2	280	43,214	0,960	0,922
Bizerta		2	31	35	23	7	2				100	42,080	1,041	1,084
Tunis	3	26	27	35	9						100	41,210	1,028	1,056

F \ t	Thau	Mauguio	Camargue	Biguglia	Ichkeul	Bizerta	Tunis
Thau	—	0,161	0,557	0,472	19,831 ++	23,619 ++	30,169 ++
Mauguio	1,101	—	0,408	0,322	20,703 ++	24,243 ++	30,935 ++
Camargue	1,053	1,045	—	0,080	20,867 ++	24,393 ++	31,024 ++
Biguglia	1,004	1,097	1,049	—	20,421 ++	24,074 ++	30,633 ++
Ichkeul	1,139	1,254	1,200	1,144	—	9,540 ++	17,030 ++
Bizerta	1,340	1,475	1,412	1,345	1,177	—	5,947 ++
Tunis	1,305	1,437 +	1,375	1,310	1,146	1,027	—

C.D.	Mauguio	Camargue	Biguglia	Ichkeul	Bizerta	Tunis
Thau	0,011	0,039 +	0,033 +	1,137 ++	1,674 ++	2,137 ++
Mauguio		0,029	0,023	1,175 +	1,723 ++	2,196 ++
Camargue			0,006	1,190 +	1,732 ++	2,201 ++
Biguglia				1,171 +	1,707 ++	2,170 ++
Ichkeul					0,567	1,008 +
Bizerta						0,420

Table IV, on the left. – Number of lower gillrakers in different lagoon populations. Table V, on the right. – Number of total gillrakers in different lagoon populations. Top: Statistical parameters. Middle: Tests of Student "t" on means and Fisher "F" on variances. Bottom: Divergence coefficient "C.D." on means and standard deviations.

Table IV – Lower Gillrakers

Lower Gillrakers	16	17	18	19	20	21	22	n	x	s	s2
Thau		2	39	44	14	1		100	18,730	0,763	0,583
Mauguio	1	3	21	48	22	5		100	19,020	0,921	0,848
Camargue		3	18	53	26			100	19,020	0,752	0,565
Biguglia		15	33	40	10			100	18,510	0,937	0,879
Ichkeul	1	21	102	130	57	11	2	324	18,809	0,967	0,935
Bizerta			6	31	51	10	2	100	19,710	0,808	0,652
Tunis		5	67	187	148	27	2	436	19,300	0,860	0,739

F \ t	Thau	Mauguio	Camargue	Biguglia	Ichkeul	Bizerta	Tunis
Thau	—	2,424 +	2,707 ++	1,820	0,842	8,817 ++	6,571 ++
Mauguio	1,455	—	0,000	3,881 ++	1,983	5,633 ++	2,776 ++
Camargue	1,032	1,501 +	—	4,244 ++	2,288	6,254 ++	3,267 ++
Biguglia	1,508 +	1,037	1,556 +	—	2,763 ++	9,697 ++	7,715 ++
Ichkeul	1,604 ++	1,103	1,656 ++	1,064	—	9,292 ++	7,260 ++
Bizerta	1,119	1,300	1,155	1,347	1,434 +	—	4,523 ++
Tunis	1,268	1,147	1,308	1,189	1,266 +	1,133	—

C.D.	Mauguio	Camargue	Biguglia	Ichkeul	Bizerta	Tunis
Thau	0,172	0,191	0,129	0,045	0,624 +	0,351
Mauguio		0,000	0,274	0,112	0,399	0,157
Camargue			0,302	0,123	0,442	0,174
Biguglia				0,157	0,688 +	0,440
Ichkeul					0,508 +	0,269
Bizerta						0,246

Table V – Total Gillrakers

Total Gillrakers	23	24	25	26	27	28	29	30	31	n	x	s	s2
Thau		1	33	33	23	9	1			100	26,090	1,026	1,052
Mauguio	1	5	16	36	27	10	5			100	26,330	1,215	1,476
Camargue	2	2	19	42	27	8				100	26,140	1,015	1,031
Biguglia		1	17	25	36	15	4	2		100	25,670	1,190	1,415
Ichkeul	1	26	81	104	73	27	10	1	1	324	26,093	1,248	1,558
Bizerta			2	24	26	40	6	2		100	27,300	1,030	1,061
Tunis		11	59	129	129	81	23	4		436	26,677	1,201	1,442

F \ t	Thau	Mauguio	Camargue	Biguglia	Ichkeul	Bizerta	Tunis
Thau	—	1,510	0,346	2,674 ++	0,021	8,325 ++	4,992 ++
Mauguio	1,403 +	—	1,200	3,882 ++	1,697	6,090 ++	2,582 ++
Camargue	1,020	1,432 +	—	3,005 ++	0,386	8,021 ++	4,602 ++
Biguglia	1,345	1,043	1,372	—	3,069 ++	10,360 ++	7,622 ++
Ichkeul	1,481 +	1,056	1,511 +	1,101	—	9,725 ++	6,487 ++
Bizerta	1,008	1,392 +	1,029	1,334	1,469 ++	—	5,282 ++
Tunis	1,371	1,024	1,399 +	1,019	1,080	1,360 +	—

C.D.	Mauguio	Camargue	Biguglia	Ichkeul	Bizerta	Tunis
Thau	0,107	0,024	0,190	0,001	0,589 ++	0,264
Mauguio		0,085	0,274	0,096	0,432 ++	0,144
Camargue			0,213	0,021	0,567 ++	0,242
Biguglia				0,173	0,734 ++	0,421
Ichkeul					0,530 ++	0,239
Bizerta						0,279

Table VI, on the left. – Number of upper gillrakers in different lagoon populations. Table VII, on the right. – Number of rays at the first dorsal fin in different lagoon populations. Top: statistical parameters. Middle: Tests of Student "t" on means and Fisher "F" on variances. Bottom: Divergence coefficient "C.D." on means and standard deviations.

Upper Gillrakers	6	7	8	9	n	x	s	s2
Thau	1	62	37		100	7,360	0,503	0,253
Mauguio	2	66	31	1	100	7,310	0,526	0,277
Camargue	5	78	17		100	7,120	0,456	0,208
Biguglia	4	76	20		100	7,160	0,465	0,217
Ichkeul	13	211	95	5	324	7,284	0,562	0,315
Bizerta		41	59		100	7,590	0,494	0,244
Tunis	16	251	158	11	436	7,376	0,599	0,359

Dorsal 1	5	6	7	8	9	10	n	x	s	s2
Thau		1	36	47	16		100	7,780	0,719	0,517
Mauguio		1	32	54	13		100	7,790	0,671	0,450
Camargue		3	50	42	5		100	7,490	0,643	0,414
Biguglia		6	43	45	5	1	100	7,520	0,731	0,535
Ichkeul		8	39	40	12	1	100	7,590	0,842	0,709
Bizerta		8	51	28	11	2	100	7,480	0,870	0,757
Tunis	2	17	59	21	1		100	7,020	0,710	0,505

Table VI — Middle (upper triangle = t, lower triangle = F):

F \ t	Thau	Mauguio	Camargue	Biguglia	Ichkeul	Bizerta	Tunis
Thau		0,687	3,535 ++	2,917 ++	1,284	3,262 ++	0,276
Mauguio	1,095		2,728 ++	2,134 +	0,425	3,878 ++	1,101
Camargue	1,216	1,332		0,614	2,968 ++	6,989 ++	4,751 ++
Biguglia	1,166	1,276	1,043		2,212 +	6,331 ++	3,948 ++
Ichkeul	1,247	1,139	1,516 +	1,453		5,235 ++	2,170 +
Bizerta	1,036	1,134	1,175	1,126	1,291		3,744 ++
Tunis	1,419 +	1,296	1,726 ++	1,654 ++	1,138	1,470 ++	

Table VII — Middle (upper triangle = t, lower triangle = F):

F \ t	Thau	Mauguio	Camargue	Biguglia	Ichkeul	Bizerta	Tunis
Thau		0,102	3,006 ++	2,535 +	1,716	2,658 ++	7,519 ++
Mauguio	1,149		3,228 ++	2,721 ++	1,858	2,821 ++	7,881 ++
Camargue	1,249	1,087		0,308	0,944	0,092	4,904 ++
Biguglia	1,035	1,189	1,292		0,628	0,352	4,904 ++
Ichkeul	1,371	1,576	1,713 ++	1,325		0,908	5,174 ++
Bizerta	1,465 +	1,683 ++	1,829 ++	1,415 +	1,068		4,095 ++
Tunis	1,025	1,121	1,219	1,060	1,405 +	1,501 +	

Table VI — C.D.:

C.D.	Mauguio	Camargue	Biguglia	Ichkeul	Bizerta	Tunis
Thau	0,049	0,250	0,207	0,071	0,231	0,015
Mauguio		0,193	0,151	0,024	0,274	0,059
Camargue			0,043	0,161	0,495	0,243
Biguglia				0,121	0,448	0,203
Ichkeul					0,290	0,079
Bizerta						0,196

Table VII — C.D.:

C.D.	Mauguio	Camargue	Biguglia	Ichkeul	Bizerta	Tunis
Thau	0,007	0,213	0,179	0,122	0,189	0,532
Mauguio		0,228	0,193	0,132	0,201	0,557
Camargue			0,022	0,067	0,007	0,347
Biguglia				0,045	0,025	0,347
Ichkeul					0,064	0,367
Bizerta						0,291

Table VIII, on the left. – Number of rays at the second dorsal fin in different lagoon populations. Table IX, on the right. – Number of rays at the pectoral fin in different lagoon populations. Top: Statistical parameters. Middle: Tests of Student "t" on means and Fisher "F" on variances. Bottom: Divergence coefficient "C.D." on means and standard deviations.

Dorsal 2	9	10	11	12	13	14	n	x	s	s2
Thau	1	8	54	34	3		100	11,300	0,704	0,495
Mauguio	1	10	56	31	2		100	11,230	0,694	0,482
Camargue		9	52	34	5		100	11,350	0,716	0,513
Biguglia		5	60	31	3	1	100	11,350	0,672	0,452
Ichkeul		1	46	41	9	3	100	11,670	0,779	0,607
Bizerta		6	56	34	2	2	100	11,380	0,722	0,521
Tunis		9	59	29	2	1	100	11,270	0,694	0,482

Pectorals	12	13	14	15	16	n	x	s	s2
Thau		12	56	31	1	100	14,210	0,656	0,430
Mauguio		13	57	29	1	100	14,180	0,657	0,432
Camargue	1	4	46	45	4	100	14,470	0,688	0,474
Biguglia		16	60	22	2	100	14,100	0,674	0,455
Ichkeul	6	106	142	25	1	280	13,675	0,681	0,464
Bizerta	5	56	36	3		100	13,370	0,630	0,397
Tunis	14	72	12	2		100	13,020	0,586	0,343

Table VIII — Middle (upper triangle = t, lower triangle = F):

F \ t	Thau	Mauguio	Camargue	Biguglia	Ichkeul	Bizerta	Tunis
Thau		0,708	0,498	0,514	3,524 ++	0,794	0,304
Mauguio	1,027		1,203	1,242	4,216 ++	1,498	0,407
Camargue	1,036	1,064		0,000	3,023 ++	0,295	0,802
Biguglia	1,095	1,066	1,135		3,109 ++	0,304	0,828
Ichkeul	1,227	1,260	1,184	1,343		2,731 ++	3,833 ++
Bizerta	1,052	1,080	1,015	1,152	1,166		1,099
Tunis	1,027	1,000	1,065	1,066	1,260	1,081	

Table IX — Middle (upper triangle = t, lower triangle = F):

F \ t	Thau	Mauguio	Camargue	Biguglia	Ichkeul	Bizerta	Tunis
Thau		0,323	2,735 ++	1,169	6,932 ++	9,236 ++	13,535 ++
Mauguio	1,005		3,047 ++	0,849	6,532 ++	8,896 ++	13,177 ++
Camargue	1,102	1,097		3,839 ++	9,940 ++	11,786 ++	16,042 ++
Biguglia	1,058	1,053	1,042		5,395 ++	7,908 ++	12,090 ++
Ichkeul	1,079	1,074	1,022	1,020		4,066 ++	9,184 ++
Bizerta	1,083	1,088	1,194	1,146	1,168		4,068 ++
Tunis	1,254	1,259	1,382	1,327	1,352 +	1,158	

Table VIII — C.D.:

C.D.	Mauguio	Camargue	Biguglia	Ichkeul	Bizerta	Tunis
Thau	0,050	0,035	0,036	0,249	0,056	0,021
Mauguio		0,085	0,088	0,299	0,106	0,029
Camargue			0,000	0,214	0,021	0,057
Biguglia				0,221	0,022	0,059
Ichkeul					0,193	0,271
Bizerta						0,078

Table IX — C.D.:

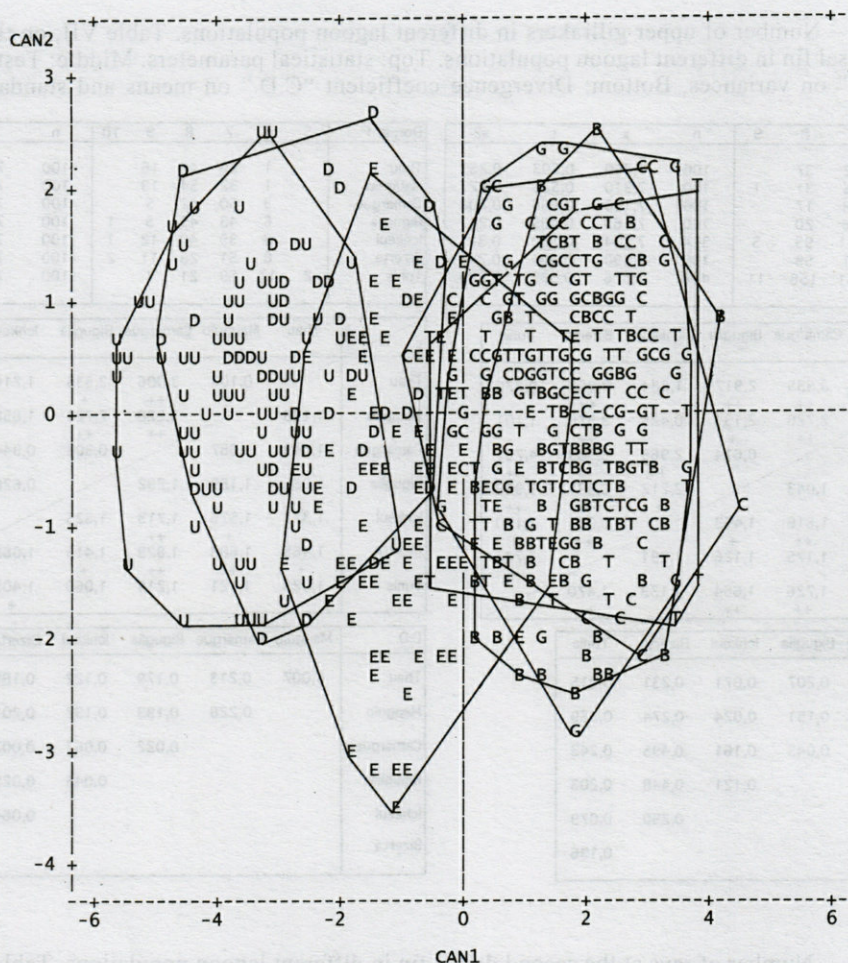| C.D.	Mauguio	Camargue	Biguglia	Ichkeul	Bizerta	Tunis
Thau	0,023	0,193	0,083	0,400	0,653	0,958 +
Mauguio		0,216	0,060	0,377	0,629	0,933 +
Camargue			0,272	0,581	0,835 +	1,138 +
Biguglia				0,314	0,560	0,857 +
Ichkeul					0,233	0,517
Bizerta						0,288

Fig. 2. – Graphical representation of canonical variables in discriminative canonical analysis of meristic characters according to axis 1 and 2. Sampling stations: France: Thau (T), Mauguio (G), Camargue (C), Biguglia (B), Tunisie: Ichkeul (E), Bizerta (D) and Tunis (U).
Axis 1: Positive part correlated with: VE, SC and PE. Axis 2: Positive part correlated with: LG and TG, Negative part correlated with: D2.

For this character (gillrakers), Bizerta and Tunis populations outstand by the highest mean values; the Ichkeul population, associated to the French sand smelts, presents lower values.

Fin rays (D1, D2, AN, PE)

For D1, the Tunis sand smelts outstand by the lowest mean value (7.0), the other populations form two overlapping groups (Tables I, VII).

For D2, Ichkeul outstands by its highest mean number (11.67); the other populations form, between themselves, a homogeneous group (Tables I, VIII).

Pectorals (PE) clearly separate, on the one hand, the French lagoon sand smelts from those of Tunisia, and, on the other hand, the latter between themselves. For this character PE, the ray mean numbers are higher among the French lagoon popu-

lations (14.1-14.5) than among those of Tunisia (13.0-13.7) (Tables I, IX).

AN does not discriminate any one of the analysed populations (Tables I, X).

Discriminative canonical analysis

The first three axes of the discriminative canonical analysis absorb 98.59% of the total variation.
– The first canonical component (93.91% of total inertia) is defined by the parameters SC, VE and PE (on the positive side);
– Axis 2 (3.03%) is correlated, positively, to the LG, TG characters and, negatively, to D2;
– Axis 3 (absorption=1.65%) is defined, positively, by D1 and UG and, negatively, by AN.
The projection of canonical variables on the plane defined by axes 1 and 2 of the discriminative canonical analysis forms two relatively distinct clouds according to axis 1.

Table X. – Number of rays at the anal fin in different lagoon populations. Top: Statistical parameters. Middle: Tests of Student "t" on means and Fisher "F" on variances. Bottom: Divergence coefficient "C.D." on means and standard deviations.

Anal	11	12	13	14	15	16	n	x	s	s2
Thau	2	12	38	42	6		100	13,380	0,850	0,723
Mauguio		19	51	27	3		100	13,140	0,752	0,566
Camargue	1	9	46	31	10	3	100	13,490	0,937	0,879
Biguglia	1	15	51	26	7		100	13,230	0,827	0,684
Ichkeul		14	35	45	4	2	100	13,450	0,857	0,735
Bizerta		13	37	48	0	2	100	13,410	0,793	0,628
Tunis	1	11	45	34	7	2	100	13,410	0,889	0,790

t \ F	Thau	Mauguio	Camargue	Biguglia	Ichkeul	Bizerta	Tunis
Thau		2,114 +	0,869	1,265	0,580	0,258	0,244
Mauguio	1,277		2,912 ++	0,805	2,718 ++	2,471 +	2,319 +
Camargue	1,216	1,553 +		2,080 +	0,315	0,652	0,619
Biguglia	1,057	1,208	1,285		1,847	1,571	1,483
Ichkeul	1,016	1,298	1,196	1,074		0,343	0,324
Bizerta	1,151	1,110	1,399 +	1,089	1,170		0,000
Tunis	1,092	1,395 +	1,113	1,155	1,075	1,257	

C.D.	Mauguio	Camargue	Biguglia	Ichkeul	Bizerta	Tunis
Thau	0,150	0,062	0,089	0,041	0,018	0,017
Mauguio		0,207	0,057	0,193	0,175	0,165
Camargue			0,147	0,022	0,046	0,044
Biguglia				0,131	0,111	0,105
Ichkeul					0,024	0,023
Bizerta						0,000

Table XI. – Values of Mahalanobis distances and of the significance "F" test between the lagoon populations. V1= d.d.l numerator and V2= d.d.l denominator.

STATIONS	ni	nj	p	D2	"F"	Significance
(GT)	100	100	9	0,25656	1,3677	NS
(GTB)	100	100	9	0,44333	2,3634	S
(GTBC)	100	100	9	0,81634	4,3520	HS
(DU)	100	100	9	1,93786	10,3309	HS
(DUE)	100	100	9	6,63558	35,3749	HS
(GTBC) (DUE)	100	100	9	15,06496	80,3126	HS

– The cloud, on the positive side, including individuals characterized by high mean values for the most discriminative meristic characters (SC, VE, PE), corresponds to the French lagoon sand smelts (Thau (T), Mauguio (G), Camargue (C), Biguglia (B)).
– The other cloud, on the negative side of axis 1, comprising specimens with lower mean values, corresponds to the Tunis (U) and Bizerta (D) populations. The Ichkeul (E) population occupies an intermediate position closer to the French sand smelts (Fig. 2).

Mahalanobis dendrogram

The Mahalanobis dendrogram significantly divides (HS) the studied populations into two clearly distinct groups (D2=15.07 HS) (Fig. 3 , Table XI).
– The first, comprising the French lagoon sand smelts (Thau (T), Mauguio (G), Camargue (C), Biguglia (B)), is characterized by high mean values for the most discriminative meristic characters (SC, VE, PE). The Mauguio (G) and Thau (T) populations show higher affinities between themselves (D2=0.26 NS) than with those of Biguglia (D2=0.44 HS) and Camargue (D2=0.82 HS).
– The second, including sand smelts with lower means, corresponds to the Tunisian lagoon popula-
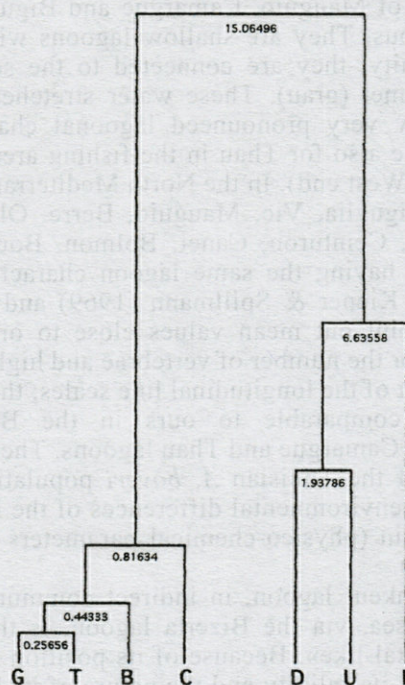
Fig. 3. – Mahalanobis dendrogram. Sampling stations: France: Thau (T), Mauguio (G), Camargue (C), Biguglia (B), Tunisia: Ichkeul (E), Bizerta (D) and Tunis (U).

tions (Tunis(U), Bizerta (D), Ichkeul (E)). The Tunis (U) and Bizerta (D) sand smelts show greater affinities among themselves (D2=1.94 S) than the Ichkeul (E) population (D2=6.64 HS).

DISCUSSION, CONCLUSION

Of the set of the meristic characters studied, only the numbers of longitudinal line scales (SC), vertebrae (VE) and the pectoral fin rays (PE) permit to distinguish the Mediterranean lagoon populations. They clearly distinguish the French sand

smelts group (Thau (T), Mauguio (G), Camargue (C), Biguglia (B)) from that of the Tunisian lagoon sand smelts (Tunis (U), Bizerta (D), Ichkeul (E)). These results indicate the presence of South-North clines for the VE and SC characters and North-South one for PE.

The multidimensional analyses (discriminative canonical analysis and Mahalanobis distances) reinforce the results obtained by the analysis when the characters were taken separately (Student "t", Fisher "F", Duncan "D" tests and Mayr-Linsley-Usinger divergence coefficient "C.D."). The relative homogeneity among the French lagoon populations is very probably due to the similarity of their environmental conditions. The physico-chemical affinities of Mauguio, Camargue and Biguglia are conspicuous. They are shallow lagoons with variable salinity; they are connected to the sea by a long channel (grau). These water stretches therefore show very pronounced lagoonal characters; this is true also for Thau in the fishing area of the samples (West end). In the North Mediterranean lagoons (Biguglia, Vic, Mauguio, Berre, Olivier 1, Olivier 2, Ceinturon, Canet, Bolmon, Bourdigou, Leucate), having the same lagoon characters, the works of Kiener & Spillmann (1969) and Marfin (1982) point out mean values close to or higher than 44 for the number of vertebrae and higher than 45 for that of the longitudinal line scales; these values are comparable to ours in the Biguglia, Mauguio, Camargue and Thau lagoons. The heterogeneity of the Tunisian *A. boyeri* populations reflects the environmental differences of the lagoons they live in (physico-chemical parameters and topography).

– The Ichkeul lagoon, in indirect communication with the sea, via the Bizerta lagoon, is the most «continental-like». Because of its position relative to the sea, its salinity and the nature of its bottom, the Ichkeul lagoon is more similar to the French lagoons; it is shallow, its salinity is relatively low during a long period of the year and the temperature variations are important. The fact that some of its characters are comparable to those of the northernmost lagoons (Biguglia, Vic, Mauguio, Berre, Olivier 1, Olivier 2, Ceinturon, Canet, Bolmon, Bourdigou, Leucate) may explain the stronger or lower affinities between geographically distant populations. Therefore, for the VE, SC and PE characters, the Ichkeul sand smelts are, among the Tunisian sand smelts, closest to the French populations.

– The Bizerta lagoon, due to its open connection with the sea, is the most «marine» one, and, be-

cause of its depth, thermal variations are more blurred. We may note the similarity of the vertebrae means of the Bizerta lagoon sand smelts (42.2) and those of Diana in Corsica (42.4) (Kiener & Spillmann 1969), which outstands by its depth and its marine conditions.

– The Tunis lagoon is shallow and very salty; its temperature is fluctuating and relatively high. The weak means of the number of vertebrae (41.2) and scales (41.2) of the Tunis lagoon population are not very different from those indicated by Kiener & Spillmann (1969) for the population of the shallow Porto-Vecchio (Corsica) salt marsh.

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CONTRIBUTIONS TO THE RUNCINIDAE.II. THREE NEW SPECIES AND COMPARATIVE STUDIES ON FIVE ESTABLISHED SPECIES OF *RUNCINA* (OPISTHOBRANCHIA CEPHALASPIDEA) IN THE MEDITERRANEAN

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RUNCINA
OPISTHOBRANCHIA
MEDITERRANEAN
RADULA
ORAL ARMATURE
SEM

ABSTRACT. – Three new species are described: *Runcina hornae* n. sp. is elongated rectangular and all over orange with a discontinuous white cross-band behind the eyes; *R. rotunda* n. sp. is plump and black with white spots bordering weakly notum and foot and densely the tail; *R. elongata* n. sp. is very slim and middle brown with a dark brown granulation, some larger dark brown spots on the head and a clear tail. An account is given of *R. coronata* (Quatrefages, 1844); *R. adriatica* Thompson, 1980; *R. africana* Pruvot-Fol, 1953; *R. brenkoae* Thompson, 1980; and *R. ferruginea* Kress, 1977; with further details on live coloration, radula and jaws by SEM. For the first time *R. coronata* is redescribed from the locus typicus, the Bretagne (France), since its original description. A synopsis of the world's Runcinacea is given.

RUNCINA
OPISTHOBRANCHIA
MÉDITERRANÉE
RADULA
ARMATURE BUCCALE
MICROSCOPIE À BALAYAGE

RÉSUMÉ. – Trois nouvelles espèces sont décrites : *Runcina hornae* n.sp., rectangulaire et allongée, entièrement orange avec une bande transversale blanche à l'arrière des yeux ; *R. rotunda* n.sp. est trapue et noire avec des points blancs espacés au bord du notum et du pied et rapprochés sur la queue ; *R. elongata* n. sp. est très grêle, brun moyen avec des granulations brun foncé, quelques taches marron foncé plus larges sur la tête et une queue claire. Une revue à propos de *R. coronata* (Quatrefages, 1844) ; *R. adriatica* Thompson, 1980 ; *R. africana* Pruvot-Fol, 1953 ; *R. brenkoae* Thompson, 1930 ; et *R. ferruginae* Kress, 1977 est donnée, avec de nouveaux détails sur la coloration sur le vivant, la radula et les machoires vues au MEB. *R. coronata* est redécrite pour la première fois depuis sa description originale à partir de la station type de Bretagne (France). Un synopsis des Runcinacea du Monde est dressé.

To the late T.E Thompson

INTRODUCTION

In the Runcinidae (Burn, 1963) there are some very well analysed species. On the other hand there are many genera and species incompletely analysed and sometimes comprising only one specimen. Therefore it is difficult to determine which character state is plesiomorphic and which is apomorphic. Synapomorphic in this group are the undivided notum, four gizzard plates (see Schmekel & Cappellato 2001), and the terminal and median anus. The first cladistically generated, testable morphology-based phylogeny for cephalaspids has been recently developed by Mikkelsen (1996).

Studies on this question are in progress (Schmekel, Cappellato & Wägele).

In this paper we describe two new species based on only one specimen: *Runcina rotunda* n. sp. only one specimen out of four could be fixated, *R. elongata* n.sp. and a third species, *R. hornae* n.sp., comprising four specimens. For the first time we redescribe the dark type species *R. coronata* (Quatrefages, 1844) from very near the locus typicus, Roscoff, with SEM micrographs of jaws and radula, and give new SEM data on the very common *R. adriatica* Thompson, 1980, and *R. brenkoae* Thompson, 1980, *R. africana* Pruvot-Fol, 1953, and *R. ferruginea* Kress, 1977, all refound at Banyuls. The characteristic features of all nine new

species and the already established species reported here are given (Table I), plus a brief synopsis of the diagnostic features of the world's Runcinacea. In part I of this work the reader can find a diagnosis of the Runcinacea (Odhner, 1939), the Runcinidae (Burn, 1963) and the genus *Runcina* Forbes & Hanley, 1853, and an extensive introduction to the morphology with new SEM facts on jaws and radula. Part I (Schmekel & Cappellato 2001) contains the description of six new species, *R. langei* Schmekel & Cappellato, 2001; *R. kressae* Schmekel & Cappellato, 2001; *R. hansbechi* Schmekel & Cappellato, 2001; *R. nivale* Schmekel & Cappellato, 2001; *R. banyulensis* Schmekel & Cappellato, 2001; *R. avellana* Schmekel & Cappellato, 2001.

MATERIAL AND METHODS: see Schmekel & Cappellato 2001. Abbreviations: b.: broad; comp.: compare; c.p.d.: critical point dried; fix.: fixated; h.: height; l.: length; Lab.: Observatoire; Mus.: Museum; rad.: radula; spec.: specimen; w.: width

RESULTS

Runcina hornae n. sp. (Pl. Ic,IIa-h,Table I; Pl. IIb/ part I).

Material: 4 specs., 1.2–2.1 mm l., Banyuls, Racou, March 30th, 1996, *Posidonia* rhizomes dredged at night at 5–8 m depth (loc. typ.). Holotype at Senckenberg Mus., Frankfurt, N° 322857.

Living holotype (Pl Ic) 2.1 mm l., 0.6 mm w., and 0.3 mm h., tail 0.5 mm. Body shape elongated rectangular, widest at the rear. Notum smooth, distinct head lobes, notum rear tapered and slightly raised. Eyes small, rather dorsal and close to the buccal mass. Foot as wide as notum, tail long, slightly pointed. Anus terminal and median, one rounded, small and inconspicuous gill lamina to the right of it. Common genital orifice not detectable.

Animal (Pl. Ic) bright orange all over, resulting from a dense sprinkling of sandy, finest brown specks on a transparent yellow ground colour. Transparent anterior notum rim narrowly coloured in a more intensive orange without any brown sand. Viscera darker orange. Two triangular fields of small white spots, pointing at each other, behind the eyes, almost connected by a few smaller fields of white spots to form a thin, discontinuous cross-band (Pl. IIb/part I). Notum rear narrowly bordered with white spots. More minor fields of white spots along the median line of the notum and its lateral margins, sparsely on the flanks of the tail, and laterally at its base. Brown sand accumulated to form a distinct brown blotch on both sides of the notum rear. Smaller brown blotches anteriorly and posteriorly to the white triangles at the notal margins, another one on either side at the base of the tail. Tail slightly lighter than the body. No notable varieties among the 4 animals found.

Anatomy: Reverse side of jaws (Pl. IIa, f) of an animal of 0.8 mm (fix), set with saucer-shaped scales of 1–3 μm diameter and a row of 9 plates with mostly 4 pointed prongs (3–4 μm l., 1.5 μm strength).

Radula (Pl. IIb-e): 15 × 1.1.1 (spec. fix. 0.8 mm, rad. l. 170 μm). Rachidian teeth (21 μm w.) bilobed (Pl. IIc–d); each flat cusp with up to 14–15 dense, parallel, fine and pointed denticles of equal length (0.3 μm l.), their tips forming a slight arc which does not run down very far onto both sides (Pl. IId). A shallow and narrow central depression, mostly without central denticle; some teeth with a very small one. Sides (17 μm l.) slightly tilted inward forming lobes. Laterals (Pl. IIe) smooth, blunt, swan-necked (16 μm h.), with a long basal region (20 μm) forming a small hump. Smaller teeth more triangular, larger ones more swan-necked. Another specimen, also fix. 0.8 mm, shows a "radular metamorphosis" (Pl. IIa) in Thompson's sense (see introduction of part I), the juvenile part with the formula 4 or 5 × 1.0.1, teeth measuring 10 × 15 μm, the adult part with the formula 4 × 1.1.1 (lateral teeth 10 μm × 5 μm). Cusps of juvenile teeth 3 × higher than those of adult lateral teeth!

4 quadrangular gizzard plates (Pl. IIh) of 90 μm l. in the specimen with only an adult radula, and 50 μm l. in the one showing "radular metamorphosis". The larger plates have 7-8 lamellae, the smaller ones 5. Very low basal beam, leaving two third of the 3-tipped lamellae free. No shell detectable by NaOH maceration or in histological sections.

Etymology: This species is named with love and sincere thanks for the sister of L. Schmekel, Mrs. Barbara Horn, Birmingham, GB for her continual help throughout the years.

Discussion: There are eight species world-wide that have a yellowish, orange or brown coloration. The chocolate brown *R. avellana* has clear head sides and front and a dark mark on the tail. All these features are lacking in *R. hornae*. The closest similarity of *R. hornae* is to *R. ferruginea* Kress, 1977 from Plymouth. They are rather similar in shape and their red colour but *R. ferruginea* never shows opaque white, which is abundant in *R. hornae*. In *R. ferruginea* the jaws show 7 rectangular plates with 7 very small prongs each, whereas *R. hornae* has 9 plates with 4 long prongs each (Pl. VIh, IIg). The radular formula of *R. ferruginea* is 24 × 1.1.1 (1 mm spec.), but the one of *R. hornae* 15 × 1.1.1 (0.8 mm spec.). The sides of the rachidians of *R. ferruginea* are upright (Pl. VIe), in *R. hornae* they are tilted slightly inwards (Pl. IIc). The denticles on the cusps laterally run much further down in *R. ferruginea* (Pl. VIf) than in *R. hornae* (Pl. IId). In *R. ferruginea* the bases of the laterals show a distinct hump (Pl. VIg), almost missing in *R. hornae* (Pl. IIe). *Lapinura* (*Ildica*) *divae* (du Bois-Reymond Marcus & Marcus, 1963; syn. *Lapinura divae* Marcus & du Bois-Reymond Marcus, 1970; *Runcina divae* Clark, 1984), from Curaçao, is brown with a light mantle furrow, while *R. hornae* is more orange. *L. divae* often has a veliger shell on a bilobate notum rear in the adult,

Table I. – Synopsis of nine new species and five established species of *Runcina* from the Mediterranean described in the two parts of this work.

Species/ loc. typ.	Our material, Distribution	Gills	Genital aperture	Jaws	Radula	Body shape	Colour
Runcina coronata (Quatrefages, 1844) Bréhat, Bretagne, F, Atlantic (1843)	5 sp. Roscoff and Plymouth. Channel, Torbay, Azores, Gibraltar, Mediterranean	2 laminae to the right of the anus, the bigger one divided into 3 archs	1/3 of the body length in front of the anus	from reverse side: rounded field with papillae, pronged plates absent	16 x 1.1.1; rach. bilobed, each with 7 thunderbolt shaped denticles, with interdenticles, narrow median depression with central denticle; lat. triangular to hook-shaped with ~ 20 denticles	3 - 7 mm; rounded all over; notum smooth, with head lobes, front of notum notched, rear rounded; foot extends notum, tail fairly long, rounded; eyes small, distantly situated	dark brown, sprinkled with minute yellowish dots; front of notum, head sides and notum rear broadly cadmium yellow, behind the eyes a narrow curve of white spots, another one in front of the notum rear; foot sole yellowish, median of tail dark brown
Runcina adriatica Thompson, 1980 Rovinj, Yug.	260 sp. Banyuls, Naples Mediterranean, Azores?	3 laminae to the right of the anus; the upper 2 subdivided horizontally	1/3 of the body length in front of the anus	triangular field with scales; unforked furrows only on one side of the scales; rim with thick bulge; 7-9 plates with 4-9 blunt prongs	25 x 1.1.1; rach. bilobed, 10 -11 denticles per pad in a curved arc, pads slightly cardium-shaped, median depression small, rarely a central denticle, the most lat. denticle stands apart, sides moderately tilted inwards; lat. smooth, short, blunt hooks, bases with small hump	0.2 - 3 mm; body quadrangular; notum smooth, front notched, with head lobes, rear tapered and raised; foot slightly extends notum, tail long, pointed; eyes medium size, rather close to the front	translucent light beige with isolated, round, blackish-brown patches all over; a broad cross band of white spots behind the eyes, more white spots densely at the notum rear, sometimes narrowly along the median, and on the sides of the tail; blackish blotches on the median of the tail
Runcina africana Pruvot-Fol, 1953 Atlantic coast of Morocco, Témara	46 sp. Banyuls Atlantic coast of Morocco, Témara; Gibraltar	3, to the right of the anus; middle lamina subdivided horizontally into 3 leaflets, the other 2 simple laminae	1/3 of the body length in front of the anus	triangular field, from reverse side with scales and buttons; 11 plates with 1-4 thick, short prongs	31 x 1.1.1; rach. bilobed, ca. 18 dense denticles per flat pad in a weak arc, median depression shallow and narrow with a pointed central denticle; lat. smooth, blunt, sickle shaped	0.3 - 2.5 mm; body elongated oval; notum smooth, front truncate, small head lobes; foot extends notum, tail broad, rounded; eyes medium size, deep, close to buccal mass	velvety dark brown on notum, foot sole and median of tail; head sides lighter brown, sometimes with oval "pseudo-eyes"; sides of tail transparent; a straight, narrow, yellowish-white cross band behind the eyes, another curved one in front of the notum end; white very variable; gills brown
Runcina brenkoae Thompson, 1980 Rovinj, Yug.	54 sp. Banyuls Rovinj, Yugoslavia, northern Adriatic coast	3 laminae to the right of the anus, middle one divided once horizontally, the other two simple	1/3 of the body length in front of the anus	triangular field with scales (from reverse side); 9 plates with 4-5 prongs	27 x 1.1.1; rach. bilobed, ca.10 denticles per pad in a distinct arc; pads cardium-shaped, median depression deep and broad, beneath it a hump, mostly without central denticle, sides long, moderately high, tilted slightly angularly inwards; lat. smooth, swannecked	0.5 - 2.5 mm; body oval; notum smooth, anteriorly tapered and notched, notum rear pointed, strongly raised; foot slightly extends notum; tail long and pointed; eyes medium size, close to buccal mass	transparent yellowish with a pattern of anastomosing dark brown patches and a marginal garland; behind the eyes two white triangulars on the sides of the notum, some white spots along its margin and rear and thickly on the sides of the tail; foot sole brownish with similar dark pattern as the dorsum; median of tail broadly dark brown
Runcina langei Schmekel & Cappellato, 2001 Banyuls-sur-mer, France	180 sp. Banyuls	2 subdivided laminae; to the right of the anus	1/3 of the body length in front of the anus	2 triangular fields with scales; unforked furrows on either side of scales, rim forms thick bulge; 9 plates with 7-9 dense, fairly pointed prongs	15 - 22 x 1.1.1; rach. bilobed, 6 - 10 regular denticles per pad in a slight arc, pads flatly cardium shaped, median depression deep and broad, some with small central denticle, sides rather high, upper edge tilted inwards; lat. smooth, scythe-shaped to swannecked, base without hump, cusp rather blunt	0.5 - 2 mm; body rounded, widest at its rear; angular head with distinct head lobes; notum rear rounded and slightly raised with a small tip, notum smooth; foot as broad as notum; eyes of medium size, in "normal" position	ground colour yellowish-green; viscera olive green with few blackish blotches; body covered all over with fine, olive green specks; behind the eyes a broad, sometimes discontinuous white cross band; notum rear broadly contoured with small white spots; 3 paired, marginal black marks close to this white pattern, repeated on the upper foot; notum and margins of tail with white spots, variable black specks in the centre of the tail; foot greenish

Table I. – (continued).

Species/ loc. typ.	Our material, Distribution	Gills	Genital aperture	Jaws	Radula	Body shape	Colour
Runcina ferruginea **Kress, 1977** Plymouth GB, Eastern Atlantic	4 sp. Banyuls, Plymouth; Mediterranean	2 laminae, to the right of the anus, subdivided horizontally into leaflets	1/3 of the body length in front of the anus	2 triangular fields, from reverse side with scales; 7 larger rectangular plates with 7 very short prongs	24 x 1.1.1; rach. bilobed, 14 -16 fine denticles per pad in an arc which is steeper medieally and runs down very far laterally; median depression small, mostly a triangular central denticle, sides short and high; lat. smooth, triangular to sickle-shaped, bases with a hump	1.5 - 2.1 mm; body elongated rectangular; anterior end of smooth notum notched, rear rounded and not raised; foot slightly broader than notum, tail long and rounded; eyes of medium size, in "normal" position	cadmium orange with a brownish tinge (Kress, 1977: reddish-brown all over), foot lighter than notum; no opaque white
Runcina kressae **Schmekel & Cappellato, 2001** Banyuls-sur-mer, France	57 sp. Banyuls		1/3 of the body length in front of the anus	2 triangular fields with scales; unforked furrows on either side, rim sharp without bulge; 6 - 7 plates with 6 -11 dense, pointed prongs	12 - 25 x 1.1.1; rach. bilobed, 10 -14 regular denticles per comb-shaped flat pad in a slight arc, median depression deep and broad, rarely a short central denticle, sides rather high and erect, upper edge hardly tilted inwards; lat. smooth, seal-necked to swannecked	0.5 - 2.5 mm; body very elongated and flat; notum smooth, anterior region fairly pointed, small head lobes; rear rounded, not raised; foot as wide as notum; tail long and rounded; eyes medium size, close to and lateral from the buccal mass	ground colour yellowish; behind the eyes a broad white cross band, notum rear broadly white, white cross band and front border of white notum end lined with black blotches thus forming 3 black cross lines, often reaching onto the foot; white spots powdered over the notum, more concentrated at notum rim, here interspersed with dark patches; middle of tail with a few dark patches; foot sole yellowish, sometimes with a few dark patches forming a cross line close to the tail
Runcina hansbechi **Schmekel & Cappellato, 2001** Banyuls-sur-mer, France	6 sp. Banyuls	2 subdivided laminae; to the right of the anus	1/3 in front of the anus	2 triangular fields with scales; scales on both sides with rather short furrows often forking, rim sharp without bulge; 11 - 12 plates, 4 - 6 very long, pointed, parallel prongs	23 x 1.1.1; rach. bilobed, 8 -10 short, pointed, regular denticles per pad in a shallow arc, pads slightly cardium-shaped, median depression deep and broad, without central denticle, sides very high, upper edge tilted inwards; lat. smooth, bluntly ducknecked, base with or without hump, cusp hollow	1.8 - 2.6 mm; body oval; notum smooth, slightly notched anteriorly, distinct head lobes, rear rounded and slightly raised; foot as wide as notum; eyes rather small, wide apart	yellowish, viscera pale orange to brownish; body densely covered with irregular large black blotches of variable shape, interspersed with sinuous fields of small white spots; pattern less intensive on foot sole; sides of tail densely white
Runcina nivale **Schmekel & Cappellato, 2001** Banyuls-sur-mer, France	2 sp. Naples	3 large laminae to the right of the anus, "bipinnate" (bigger specimen), undivided (smaller specimen)				fix. 1.4, 2 mm; body drop-shaped, widest and highest at notum rear; notum smooth; foot extends notum; tail very long, wide, rounded; notum rear of the smaller animal tapered, of the larger one bilobed; eyes very large, high and close to the front	totally transparent whitish; eyes and ganglia well visible
Runcina banyulensis **Schmekel & Cappellato, 2001** Banyuls-sur-mer, France	4 sp. Banyuls	1 lamina, subdivided slightly horizontally, to the right of the anus		reverse side: 2 triangular fields with scales and papillae; up to 10 plates, mostly 4 pointed prongs	22 x 1.1.1 rach. bilobed, 8 - 9 finger-shaped, regular denticles per flat pad in a slight arc, median depression concave, deep and broad, no central denticle, sides moderately high, upper edge angularly tilted inwards; lat. smooth, sickle-shaped, base without hump, cusp hollow	0.4 - 1.4 mm; body elongated; front of smooth notum with depression, almost no head lobes; rear long, rounded and not lifted; foot as wide as notum, tail short, rounded; eyes large, high, close to the front	yellowish, viscera beige to brown; all over with isolated, fine, sharp black points, less on the foot; notum broadly bordered with white, interspersed with red-brown points in the head region, and red points further down; a 'T' of pure white on the notum; its cross band contoured with some large black points

Table I. – (continued).

| Species/ loc. typ.	Our material, Distribution	Gills	Genital aperture	Jaws	Radula	Body shape	Colour
Runcina avellana Schmekel & Cappellato, 2001 Banyuls-sur-mer, France	3 sp. Banyuls	1 lamina, slightly to the right of the anus		reverse side: 2 triangular fields with cup-shaped scales; up to 11 plates, 8-10 pointed prongs	juvenile: 3 x 1.0.1; lat. smooth, cusp high, triangular, base short	1 - 1.5 mm; body elongated, slightly arced; notum smooth, no head lobes, front slightly notched, rear rounded, not raised; foot as wide as notum; tail long, broad, rounded; eyes small, very deep and close to the front	notum dark brown; front and sides of the head and tail transparent; some small white spots around the eyes and along the notum margins; foot sole light brown; one dark blotch in the centre of the tail
Runcina sp.	1 sp. Banyuls	1 lamina, small and simple, to the right				1.9 mm; body elongated, flat; notum smooth, front straight, scarce head lobes, notum rear slightly pointed, not raised; foot as wide as notum; tail short, rounded; eyes medium size, close to the buccal mass	velvety dark green, notum margin transparent lemon yellow, enlarged at head, foot sole and tail; sprinkled with tiny brown specks and sparse small white spots all over, more dense on notum and foot margins, especially at notum rear; a single dark green spot in the centre of the tail, a pair of similar, larger marks at its insertion
Runcina hornae Schmekel & Cappellato, n. sp. Banyuls-sur-mer, France	4 sp. Banyuls	1 leaflet, small, inconspicuous, to the right		from reverse side; 2 triangular fields with scales and buttons; up to 11 plates, 1 - 4 thunderbolt shaped, thick, short prongs	15 x 1.1.1; rach. bilobed, 10 -15 fine, pointed, dense, regular denticles per flat pad in a rather short arc; median depression shallow and narrow, rarely a small central denticle, upper edge of the sides slightly tilted inwards; lat. smooth, swannecked, base long with a small hump	1.5 - 2.1 mm; body elongate, rectangular, widest at its end; with distinct head lobes, notum smooth; foot as wide as notum; tail long, tapered; eyes small, dorsal, close to the oesophagus	yellowish with finest brown sand all over, thus appearing orange; behind the eyes a thin, discontinuous cross band of small white spots, notum rear narrowly bordered with white; small fields of white spots on notum and tail; 3 paired, small brown marks at the notum margin, adjacent to the white, 1 pair on the foot at the insertion of the tail
Runcina rotunda Schmekel & Cappellato, n. sp. Banyuls-sur-mer, France	4 sp. Banyuls	1 small, simple leaflet, to the right of the anus				1.1 mm; body plump, convex, rounded; notum smooth, slight head lobes; foot extends notum, tail short and slightly pointed; eyes not visible	black with greenish tinge, very indistinct black blotches on the viscera; notum, foot bordered narrowly and discontinuously with small white spots, some white spots in the centre of the notum and densely on the "ears"; tail colourless with dense white spots laterally
Runcina elongata Schmekel & Cappellato, n. sp. Banyuls-sur-mer, France	1 sp. Banyuls					1.2 mm; body elongated, very slim; head lobes absent, anterior notum end straight, notum rear rounded, not raised, notum smooth; foot as wide as notum, tail short, rounded; eyes medium size, extremely close to the front, deep	body middle brown all over, with fine dark brown granulation, larger dark brown spots on the head; notum margin very narrowly bordered with white; a pair of red brown patches at the insertion of the tail, tail colourless
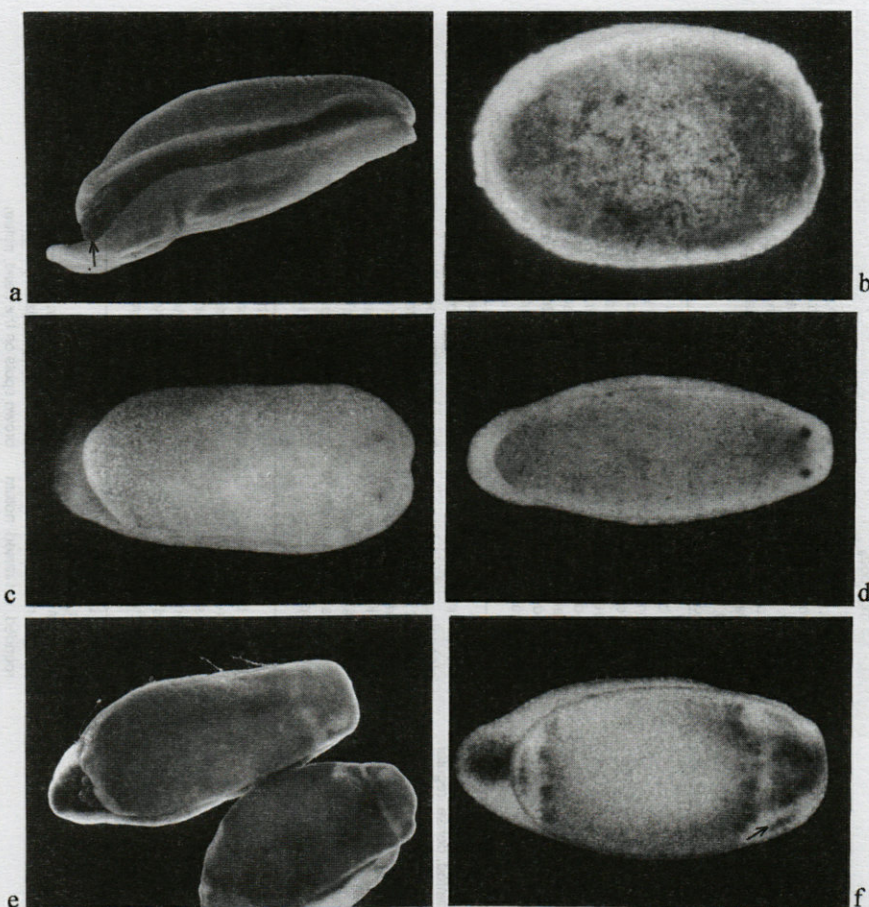
Plate I. – Light micrographs. **a**, *Runcina ferruginea* Kress, 1977, 3 mm length, from Plymouth; arrow: gills; **b**, *R. rotunda* n. sp., holotype, 0.6 mm length; specimen lost colour after fixation, revealing few irregular black blotches and a lighter notal margin; **c**, *R. hornae*, n. sp., holotype, 0.9 mm length; **d**, *R. elongata* n. sp., holotype, 1.2 mm length; **e**, *R. africana* Pruvot-Fol, 1953, 2.4 and 1.9 mm length; **f**, *R. africana*, 1.8 mm length, arrow: eye-patches.

which is absent in *R. hornae*. The denticles on the rachidians of *L. divae* form a straight cutting edge, but an arc in *R. hornae*. *R. marshae* Burn, 1966, from Fiji, is dull orange when fixated, but in contrast to *R. hornae* it has an internal shell. The reddish-brown *R.* spec found by Gosliner (1990), from the Azores, is easy to distinguish from our species by its denticulate laterals which are smooth in *R. hornae*. The ochre-coloured *R. bahiensis* Cervera, Garçía-Gomez & Garçía, 1991 from Gibraltar, in contrast to the orange *R. hornae* with a smooth notum, is covered with opaque ochre pigmentation, and the notum shows numerous small protuberances.

R. lenticula from Angola has a brown notum but unicuspidate rachidians (Gofas *et al.* 1991: 542; fig. 3: 544), in contrast to bilobate ones in *R. hornae*. *R. macfarlandi* Gosliner, 1991, from the Pacific coast of North America, has an opaque yellowish-brown notum with darker pigment in the centre, and two gill plicae standing on opposite sides of the anus, in contrast to the more transparent orange *R. hornae* whose single gill plate lies to

the right of the anus. *Runcinella thompsoni* Ortea & Rodríguez, 1993, from Galapagos, is dark red with a yellow blotch on either side of the head, whereas *R. hornae* is bright orange with opaque white spots. *R. thompsoni* has a large inner shell, and its radular formula is 1.1.1.1.1, the one of the shell-less *R. hornae* is 1.1.1.

Runcina rotunda n. sp. (Pl. Ib, Table I; Pl. IId/part I)

Material: 4 specimens, 0.7–1.1 mm l., at Banyuls, le Racou, March 28th, 1996, *Posidonia* rhizomes dredged at night at 6–11 m (loc. typ.).

This species is less vigorous than other *Runcina*; they crawl very slowly, are very fragile and die quickly in their bowls. Only one specimen could be recovered for fixation. Holotype at Senckenberg Mus., Frankfurt, No. 322858.

Description of the living holotype (Pl. IId/part I) of 1.1 mm l., 0.6 mm w., 0.4 mm h., tail 0.1 mm: Body shape plump, rounded. Smooth notum very convex, slight head lobes, rear short, rounded and slightly raised. Foot extending the notum laterally, tail very short and
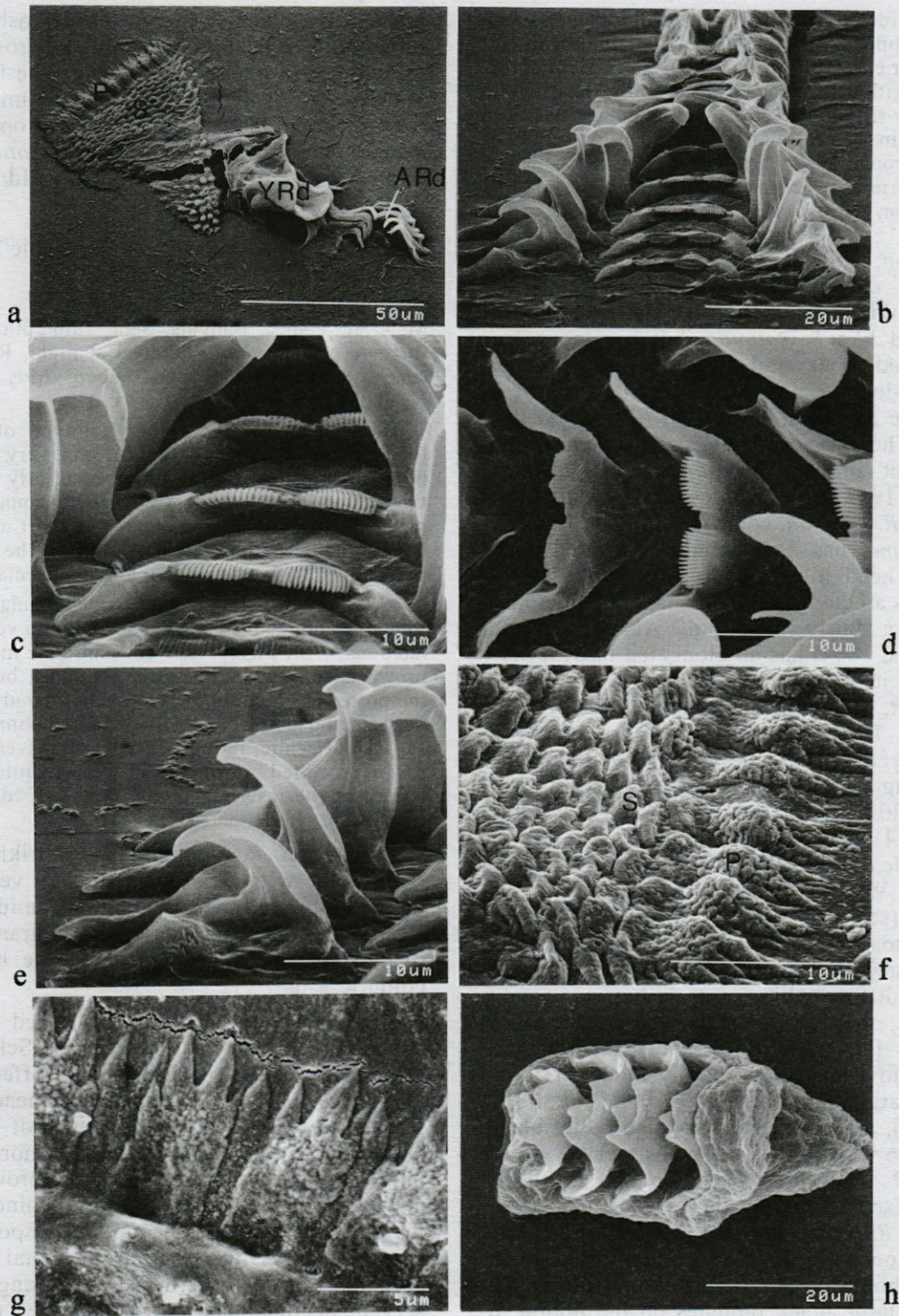
Plate II. – SEM micrographs. *Runcina hornae* n. sp., **a**, jaws, reverse side, and radula (juvenile and adult parts); P plates with prongs, S scales, YRd juvenile radula, ARd adult radula; **b**, radula, rachidian and lateral teeth; **c**, rachidian teeth; sides of rachidian teeth slightly tilted inwards; **d**, rachidian teeth with small central denticle; **e**, smooth lateral teeth; **f**, reverse side of jaws; P plates with prongs S scales; **g**, reverse side of plates with paired prongs; **h**, gizzard plate; note quadrangular shape.

slightly pointed. Eyes not visible. Anus terminal and median, one small, simple, rounded gill lamina to the right of it. Black all over with a green tinge, except the co-

lourless tail (Pl. IId/part I). Some very indistinct black blotches above the viscera which are seen better some time after fixation (Pl. IId/part I). Notum, upper foot and

foot sole bordered narrowly by small opaque white spots, discontinuous in some places and almost missing at the anterior end of the notum. Flanks of the tail covered broadly with dense opaque white spots. Small white spots sparsely scattered over the entire notum, a bit more concentrated in the centre of it. Head lobes with field of white spots, copied just beneath on the upper face of the foot sole. Varieties: the pattern of white spots may be less distinct on the notum, the foot and the tail.

Discussion. *R. calaritana*: see discussion *R. coronata*. *R. coronata* (Quatrefages 1844, see description in this article), from the Bretagne, is oval and rounded like *R. rotunda*, but has more pronounced head lobes, and its tail is much longer. The head sides, the notum rear and the foot of *R. coronata* are cadmium yellow, in *R. rotunda* they are black. The curved white cross-bands are regularly present in *R. coronata* and *R. africana* Pruvot-Fol, 1953, from Morocco, but are absent in *R. rotunda*. *R. rotunda*, compared to our specimens of *R. africana*, has a much more rounded body, very small head lobes and a very short tail. *R. africana* has an elongated oval shape, distinct head lobes and a fairly long tail. Also *R. ornata* (Quatrefages, 1844) has an elongated to oval body shape while it is plump and convex in *R. rotunda*. The tail of *R. ornata* is long, the one of *R. rotunda* very short. Though both species are black, *R. ornata* has yellowish head sides, the yellow sometimes joining behind the eyes (see Cervera *et al.* 1991: 200-201, fig. 2; Ballesteros & Ortea 1981, fig. 1B, p. 34), and a yellowish notum rear only on the right side, while *R. rotunda* is only black with some white. While *R. capreensis* Mazzarelli, 1894, from Capri (see discussion *R. hansbechi* Schmekel & Cappellato, 2001, part I) is charcoal black, covered regularly with many large, isolated black points and diffuse white spots in-between, and a yellow foot, *R. rotunda* is more homogeneously black with few very deep and obscure black blotches, and white spots mainly along the notal and foot margins. *R. zavodniki* Thompson, 1980, from Rovinj, a species that may also be jet black, lacks opaque white spots. Like Gosliner (1990) we consider *R. zavodniki* synonymous with *R. ferruginea* (see discussion there). Gosliner (1990) describes a *Runcina* from the Azores with a dark ground colour he tentatively identifies as *R. adriatica* Thompson, 1980. While Gosliner's species shows large black blotches on the notum, *R. rotunda* bears only a few very deep blotches which can be seen clearly only after fixation (Pl. Ib). The tail of the animals from the Azores is totally black, in *R. rotunda* it is transparent with opaque white spots thickly covering the sides. Gosliner's *R. adriatica* bears a broken transverse white cross-band on its notum behind the eyes and a cross-band near the notum rear. *R. rotunda* has only some opaque white laterally on the head lobes and the notal and foot margins. The pacific species *Metaruncina setoensis* (Baba, 1954), from Kii,

Japan, is blackish-brown with ashy yellow submargins of the notum running all around it, only excluding the anterior notum end. The foot sole of *M. setoensis* is lighter than the notum, in *R. rotunda* it is as black as the notum. No opaque white is mentioned for *M. setoensis* but *R. rotunda* shows a fair amount of opaque white (Pl. IId/part 1).

Runcina elongata n. sp. (Pl Id, Table I; Pl. IIf/part I)

Material: 1 spec. Banyuls, Sept. 25th/26th, 1997 from rhizomes of *Posidonia* dredged at night, Racou, 10 m (loc. typ.). Holotype: Senckenberg Mus., Frankfurt, N° 322859.

Body shape of the living holotype of 1.2 mm l., 0.5 mm w, and 0.3 mm h., tail 0.2 mm, very slim, resembling a torpedo. Smooth notum anteriorly straight without head lobes, posteriorly narrowly rounded and not raised. Foot as wide as notum; tail short and rounded. Eyes large deep and extremely close to the anterior notum end. No gill, anus or genital pore detectable (Pl Id).

Middle brown all over with a fine granulation: notum, foot sole and mantle furrow covered with very fine, isolated dark brown specks, concentrated in the lighter brown head region to form larger spots, but sparser in the posterior notal region. Notum sprinkled evenly with very fine opaque white spots, bordered slimly with denser opaque white; no opaque white transverse bands. A row of small red brown patches in the mantle furrow, the largest at the insertion of the tail. Tail colourless and translucent (Pl. IIf/part I).

Discussion. *R. elongata* has a striking torpedo body-shape with large eyes situated very close to the front (Pl. Id). It is the only middle brown *Runcina* with a fine dark brown granulation all over, somewhat larger spots on the head and a colourless tail.

Apart from the features described above, the chocolate brown *R. avellana* Schmekel & Cappellato, 2001 (Pl. IVc/part I) differs from *R. elongata* (Pl. Id) by its translucent head-sides and the single black spot in the centre of the tail. *R. hornae* (Pl. Ic; Pl. IIb/part I) has a more rectangular body shape, is orange instead of brown, and has an indistinct white cross-band behind the eyes while in *R. elongata* opaque white spots are concentrated only slightly along the notal margin. *R. marshae* from Fiji, coloured dull orange as a preserved specimen, shows an inner shell through the epidermis, which is not detectable in *R. elongata*. The all over red brown *R. ferruginea* Kress, 1977 (Pl IIn/part I), from Plymouth, has no opaque white spots whatsoever. The colour of *R. ferruginea* in Ortea & Urgorri (1981), from Northern Spain, is brown but the main difference to *R. elongata* are the "rugosités" which are absent in our species, as well as in Kress's original description of *R. ferruginea*. *R. paupera* Ortea, Rodríguez and Valdés, 1990, from Cape Verde, is rounded and greenish-brown with a translucent green notal mar-
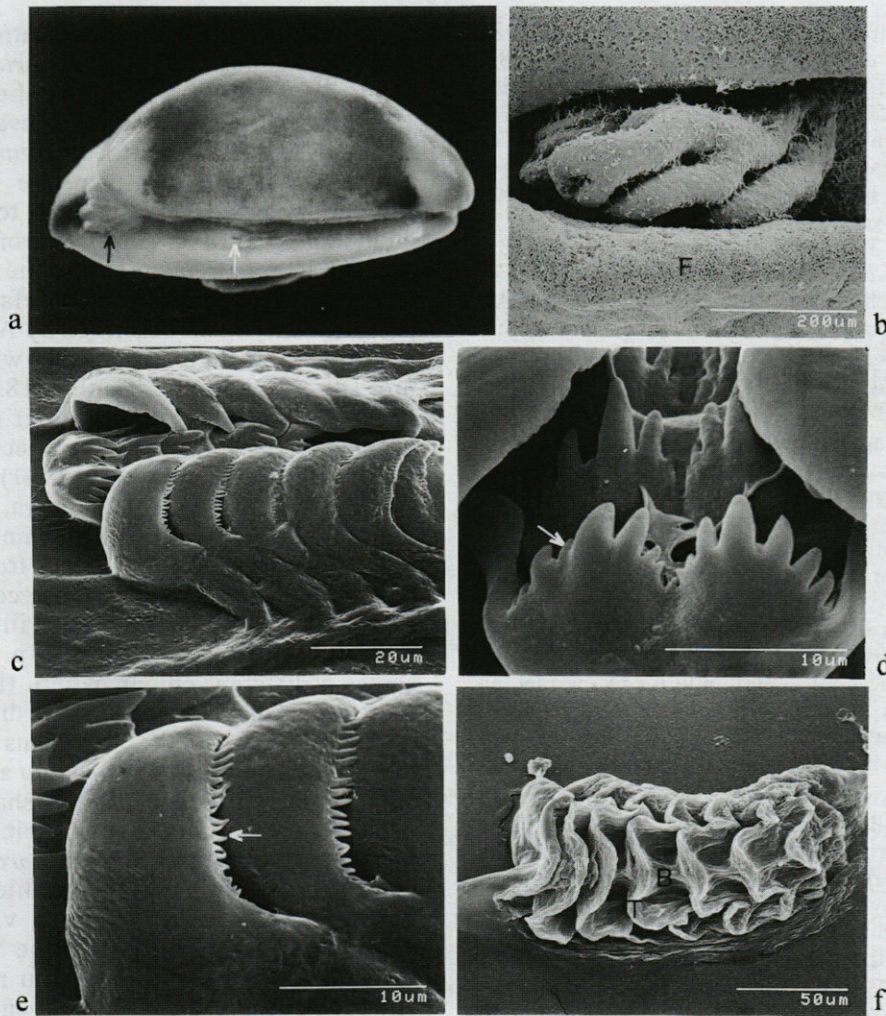
Plate III. – *Runcina coronata* (Quatrefages, 1844) from Roscoff, France. **a**, light micrograph of specimen, 5 mm length, total aspect viewed from the dorsal right side; white arrow: genital orifice, black arrow: gills; **b**, gills; F foot, SEM; **c**, radula, oldest part, SEM; **d**, rachidian teeth; arrow: interdenticle, SEM; **e**, lateral teeth; arrow: denticulate cusp, SEM; **f**, gizzard plate from above (boat shape typical for most *Runcina*); B basal beam, T lamella, SEM.

gin, without any opaque white. *R. elongata* is very elongated and slim and has a sprinkling of opaque white over the notum. The ochre-coloured *R. bahiensis* Cervera, Garçía-Gomez & Garçía, 1991 (Strait of Gibraltar) shows small protuberances on its notum, while the notum of *R. elongata* is smooth. The body shape of the brown *R. lenticula*, from Angola, is more rounded and wider than the one of *R. elongata*. The Californian *R. macfarlandi* has a broad ovoid body shape and gills on both sides of the anus. Though our specimen of 1.2 mm length has no gills, the body shape and the colour of Gosliner's (1991) species – yellowish-brown notum, darker in the centre, and no opaque white – differs clearly from *R. elongata*. *Runcinella thompsoni* Ortea & Rodríguez, 1993, from Galapagos, is dark red with a yellow blotch on either side of the head. *R. elongata* is brown with a fine darker granulation and blackish-brown spots on the head, instead. The brown *Lapinura*

(Ildica) divae (du Bois-Reymond Marcus & Marcus, 1963), from Curaçao, often has a minute external veliger shell in the adult, which is absent in *R. elongata*. While *L. divae* has a light mantle furrow, in *R. elongata* it is middle brown. The eyes are not visible in living *L. divae*, but in *R. elongata* they are conspicuous.

Runcina coronata (Quatrefages, 1844)
(Pl. IIIa-f, Table I; Pl. II l/part I)

Ann Sci Nat Zool 1: 151-152, Pl. 3, fig. VI)
Pelta coronata Quatrefages, 1844. Loc. typ.: Saint-Vast-la Hougue, Bréhat, Bretagne, collected 1842/1843, Compare Opinion 811 *Bull zool Nomencl* 1967: 89-90.
Unnamed species of Alder & Hancock 1846: 289-291, p. l. IV 1-7
Runcina hancockii Forbes & Hanley, 1853: 611-612
Most probably *Runcina calaritana* Colosi, 1914/15: 1-35

Runcina aurata Garçía, López, Luque & Cervera, 1986 (compare Cervera *et al.* 1991) (Ref. Vayssière 1883, 1885, 1900, 1903; Mazzarelli 1894; Colosi 1914/15; Pruvot-Fol 1954: 53-55, fig. 10 a-r; Thompson, 1976: 143-145, fig. 77 a-f ; Thompson & Brown 1976: 37-38, fig. 15; Kress 1977; Kress 1985a; Kress 1986; Kress & Schmekel 1992; Kress *et al.* 1994; Poizat 1978; Gosliner 1990; Cervera, Garçía-Gomez & Garçía 1991) Material: 3 specs., 3, 5 and 7 mm, Roscoff (France). 03. 1973; 4 specs., 4–7 mm, Plymouth (Great Britain), 1974: Kress (coll.) – which is all from the eastern Atlantic! All from the upper littoral fringe at low tide, Vayssière's (1883) animals are from Marseille (France), those of Cervera *et al.* (1991) from Gibraltar. We did not find it in the Mediterranean: neither in Naples nor Banyuls.

A moderately agile species. An animal (6 mm l., 2.5 mm w., 3 mm h., tail 1 mm) from Roscoff, Bretagne, very near the loc. typ. of Quatrefages (1844), has a rounded all over body shape (Pl. IIIa). Anterior notum end slightly notched with head lobes; small oral bulges. Foot broader than notum, tail rather long and rounded. Eyes small, situated wide apart in the region between the yellow sides of the head and the brown central zone (eye: Mikkelsen 1996: 401, figs. 37, 38). Common genital orifice one third of the body length anterior to the median anus (Pl. IIIa). Two rounded gill laminae to the right of the anus (Pl. IIIb; spec. c.p.d. 1.5 mm), the smaller, ventral one undivided, the larger one divided into three arcs.

Notum dark brown with very, very fine yellowish points. Anterior and posterior notal end and sides of the head a bordered broadly with cadmium yellow. At the notum rear the anterior border of the cadmium yellow region is curved away from the notum end (Pl. II l/part I). Two fine opaque white curved cross bands on the notum: one, curved away from the front, behind the eyes, one, curved in the opposite direction, anterior to the notum end. Foot sole yellowish, its upper face darker cadmium yellow; mantle furrow brown all around; gills yellowish with slightly brown margins. Yellowish tail-seen from above and below–with a broad dark brown median part.

Anatomy: Reverse side of jaws with two rounded fields (diameter 100 µm) without sharp border, set with short papillae but lacking plates with prongs.

Radula: 16 × 1.1.1 (spec. 1.5 mm fix. Plymouth, rad. l. 250 µm). Rachidian teeth bilobed, each *Cardium*-shaped pad with 7 thick, blunt and thunderbolt shaped denticles of very variable size (max. 5 µm l.); tips of each set of denticles forming a high arc. The size and strength of the denticles on each pad increase towards the centre. Some short, slender interdenticles are situated almost exclusively towards the edges of each pad, but the number of strong denticles always prevails. The only measurable tooth (28 µm w., 10 µm h. and 20 µm l.) has a central denticle (0.5 µm) in a narrow but deep depression. Laterals triangular to hook-shaped with about 20 small, pointed denticles (1–2 µm) along their cutting edge (Pl IIIc,d,e).

4 gizzard plates (Pl. III f, 160 µm.l) with 7 lamellae having 1 or 2 tips each; longitudinal beam high, leaving one third of the lamellae free. No shell detectable by NaOH maceration or in histological sections.

Discussion. The history of *R. coronata* and its name is complicated. The main reason is the existence of several dark *Runcina* species in the Eastern Atlantic and Mediterranean, which show certain similarities (*R. ornata* Quatrefages,1844); *R. calaritana* Colosi, 1914/15; *R. africana* Pruvot-Fol, 1953; *R. aurata* Garçía, López, Luque & Cervera, 1986; comp. discussions of *R. avellana* Schmekel & Cappellato, 2001; part I, *R. rotunda* Schmekel & Cappellato n. sp.) and therefore have been confused in the past. This is the first recent description including SEM of *R. coronata* from near the locus typicus, in the Bretagne. After the first description from the Bretagne by Quatrefages (1844), *R. coronata* was again described by Alder & Hancock (1846) without a given name but with very fine figures (Pl. IV). Forbes & Hanley (1853: 611–612) referred to this description in their diagnosis of the genus *Runcina* and gave the species the name *R. hancockii*. Cervera *et al.* (1991) put *R. aurata* Garçía, López, Luque & Cervera, 1986 in synonymy with *R. coronata*. The specimen on the photograph in Cervera *et al.* (1991) from Gibraltar indeed looks very similar to those collected by us in Roscoff and Plymouth. The illustrated animal (Cervera *et al.* 1991, fig. 1, p. 200), however, shows a different colour pattern (black spots on a light background) and a slightly differing structure of the denticles of the rachidians than our specimens. The laterals of *R. coronata* and *R. aurata* are very similar in their triangular shape with 20 fine denticles. We cannot give sufficient data concerning the range of variety of *R. coronata* in the waters of the Atlantic and the Mediterranean, but we do suspect *R. aurata* to be a valid species. *R. calaritana* Colosi, 1915, from the Mediterranean is black with yellowish borders on mantle and foot, enlarged at the posterior notum end. We think this species is probably synonymous with *R. coronata*: Colosi's description of *R. calaritana* is most detailed in histology and anatomy while the whole animal is not depicted. Poizat (1978, p. 137, Pl. XID) collected 296 specimens from mediolittoral rocks in the sand grounds of the Marseillan Gulf which he described as *R. coronata*. The animals in his photograph are squarer than our specimens, and the pattern of the presumable opaque white spots on the dark specimen remind us more of *R. africana* Pruvot-Fol, 1953, or *R. langei* Schmekel & Cappellato, 2001. It might even be a third species yet unknown. Gosliner (1990) described a uniformly brown *Runcina* sp. from the Azores. The rachidians of his specimens lack smaller interdenticles, and the laterals bear about 50 denticles, in contrast to about 20 in our *R. coronata* (Pl. IIIc, e; Kress 1977, Pl. IF: about 25).

Runcina adriatica Thompson, 1980 (Pl. IVa-d, Table I; Pl. IIj, IIIe,f, IVb/part I)

J moll Stud 46: 54-157, figs. 1a, b; loc. typ.: Red Island (San Andrea), Rovinj, Yugoslavia, Adria.
(Ref.: Ballesteros & Ortea 1981: 33–35 fig. 1C; Thompson & Brodie 1988: 339-346, figs. 1a, b; Gosliner 1990: fig. 1B, p. 136; fig. 5A, p.140; figs 6, 7, p. 142)
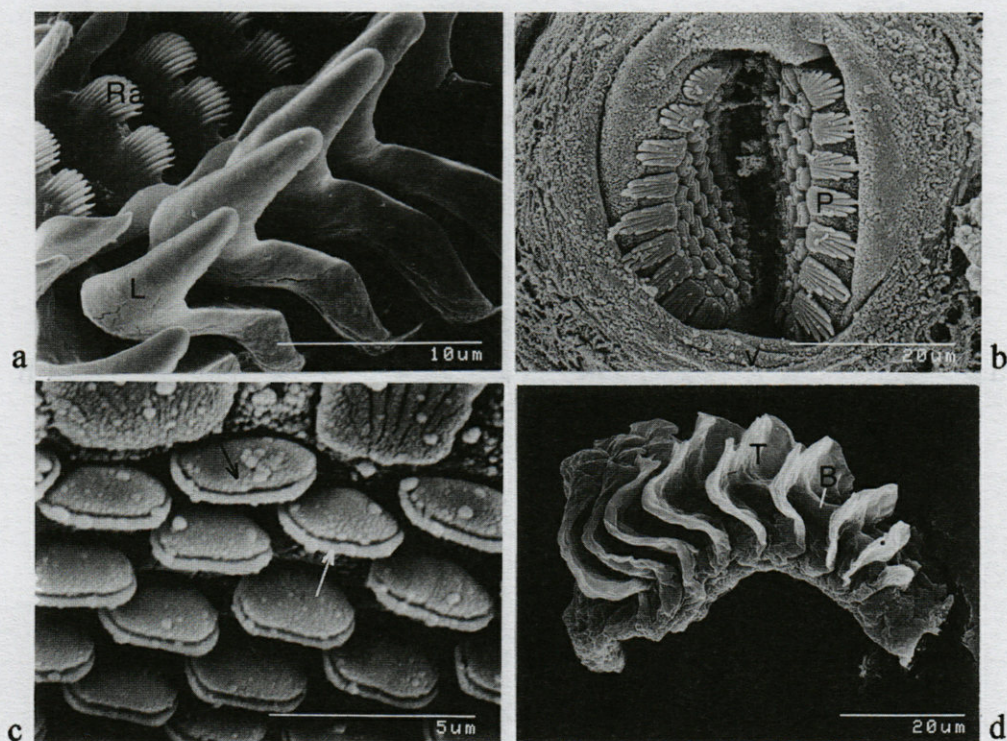
Plate IV. – SEM micrographs of *Runcina adriatica* Thompson, 1980; **a**, radula; Ra rachidian teeth, L lateral teeth; **b**, mouth with protruded jaws (hyperthermic stress method) ; P plates with prongs: note blunt tips, v ventral; **c**, scales of jaws; white arrow: bulge, black arrow: smooth side of scale facing the mouth; **d**, gizzard plate, lateral view; B basal beam, T lamellae.

Material: 260 specs., 0.2-3 mm, common at Naples and Banyuls: from Le Racou to Cap l'Abeille, 1964-1998, ca. 2-12 m depth.

A very agile, quickly crawling species. Body shape of a specimen from Banyuls, 1996 (2 mm l., 0.5 mm w., 0.4 mm h., tail 0.5 mm) squat and quadrangular (Pl. III e, f/part I), with pronounced head lobes, notum rear slightly tapered and raised. Foot as wide as notum, tail long and tapered. Eyes of medium size, deep and close to the anterior border of the head. Genital orifice one third of the body length anterior to the median anus. 3 rounded gill laminae (spec. c.p.d. 1.4 mm) to the right of the anus, the upper two subdivided horizontally, the most ventral one simple.

Body translucent yellowish to light beige; viscera mostly red-brown. Notum, foot, mantle furrow, and median of tail covered with many round to oval, dark brown to black, mostly isolated patches, in smaller animals lining mainly the notal margin and the opaque white pattern, but in larger specimens spread more evenly over the notum (Pl. IIIe/part I). Often they form a 'v', pointing to the front (Pl. IIj/part I), between the eyes. One broad, straight, opaque white cross-band behind the eyes. Notum rear broadly opaque white, with a straight border anteriorly, some more white on the sides of the tail.

Anatomy: Jaws (Pl. IVb,c; Pl. Id, IVb/part I) triangular with shell-shaped scales, broadest at the margins of the fields. Scales close to the plates with fine and parallel, vertical grooves on their side facing the gizzard, but none on the side facing the mouth, and a thick bulge along the rim. 7 to 9 large plates (7 μm), with 4 to 9 parallel blunt-tipped prongs (3 μm l.; Pl. IVb,c).

Radula (Pl. IVa; Pl. IVb/part I): 3 specs. of fix. 1.3 mm, 1.5 mm and 1.9 mm all have a radula of 25 × 1.1.1 (140 and 150 μm l.). Rachidian teeth (13 μm b. × 11 μm l.) bilobed, each flat pad with 10-11 slender, slightly diverging, pointed denticles (0.5 μm l.), the outermost shorter and a little isolated. The tips of the denticles form an arc. Mostly no central denticle in the shallow and moderately narrow central depression. Sides of rachidians moderately high, broad and tilted inwards at the upper edge. Laterals (18 μm l. 14 μm h.) smooth, blunt, short and duck-necked with slightly triangular bases forming a small hump.

Normally 4 gizzard plates with 7 to 10 lamellae (Pl. IVd) with 2 to 3 tips, but in one spec. exceptionally 5 plates (1 × 8, 3 × 9, 1 × 10 lamellae); basal beam leaving one third or more of their length free. Male copulatory organ similar to the one of *R. ferruginea* described by Kress (1985 b). No shell detectable by NaOH maceration or in histological sections (Pl. IVb, Id/part I).

Discussion. Our material is very similar to that of Thompson (1980) and Thompson & Brodie (1988). We can, however, contribute further details to the structure of the jaws of this species. The scales (Pl. IVc) of the jaws of *R. adriatica* are characteristic in having simple vertical grooves only on the side facing the gizzard, whereas the scales of *R. langei* Schmekel & Cappellato, 2001, *R. kressae* Schmekel & Cappellato, 2001 and *R. hansbechi* Schmekel & Cappellato, 2001 show grooves on both sides.
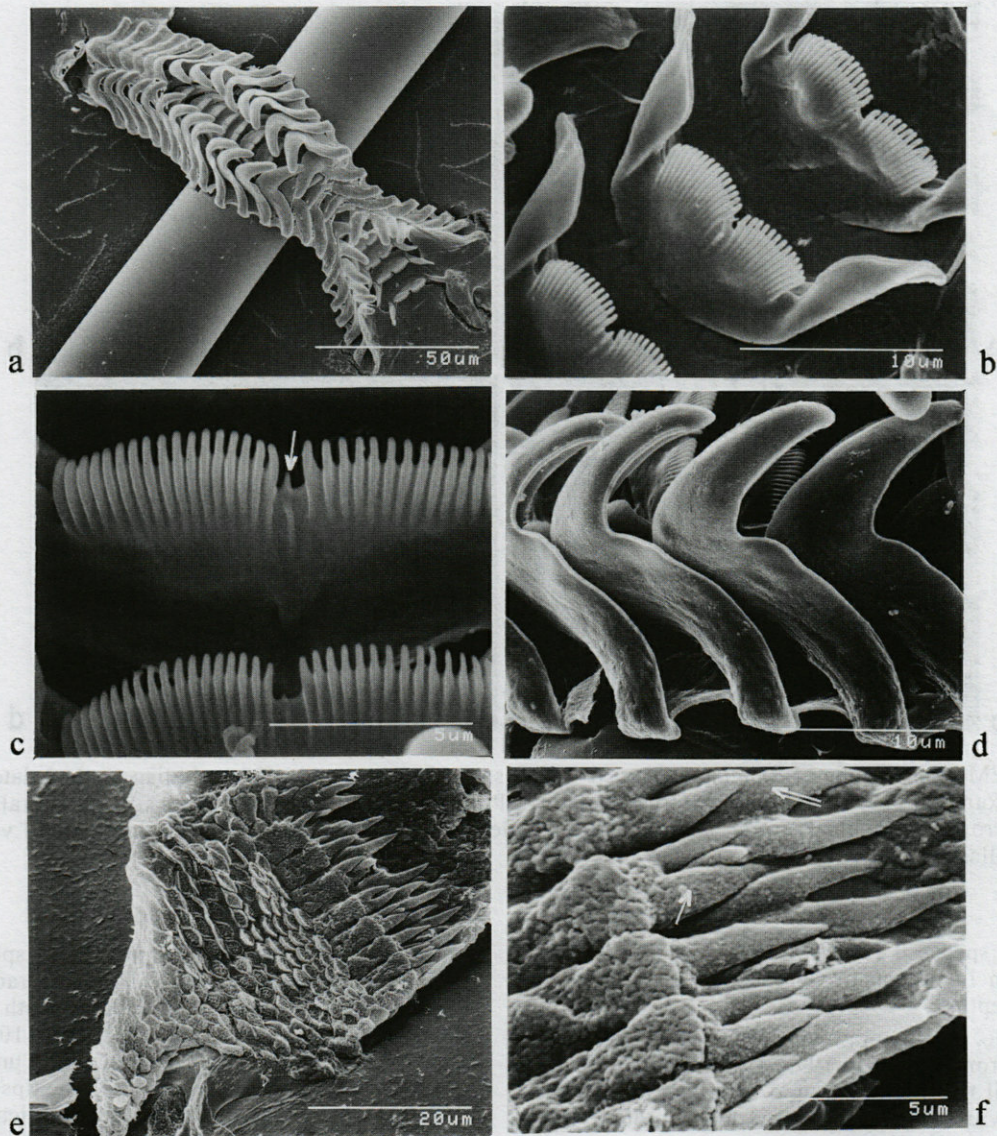
Plate V. – SEM micrographs of *Runcina africana* Pruvot-Fol, 1953. **a**, radula, placed in almost natural position on a glass thread, top view; **b**, rachidian teeth; note very narrow central depression with central denticle; **c**, detail of "b"; arrow: central denticle; **d**, lateral teeth; **e**, jaws, reverse side; **f**, plates with prongs of opposite fields of jaws; arrow: prongs from reverse side, double arrow: prongs of opposite field.

Runcina africana Pruvot-Fol, 1953 (Pl. Ie-f, Va-f, Table I; Pl IIm, Pl Ie/part I)

Trav Inst Sci Chérifien 5: 25–27., text-fig. 1, Pl. II, fig. 35; locus typicus: Témara, Atlantic coast of Morocco / Senegal, tidal zone. (Ref.: *Runcina africana* Cervera *et al.*, 199: p. 201–203, fig. 3, 6 D–F)
Material: Banyuls: 15 spec. fix. 2–2.5 mm, 05. 1958, several with up to 3 spermatophores attached: E. Sandmeier & A. Portmann (coll.); 10 spec., 0.3–2.5 mm, 05. 1986: I. Richter (coll.); 21 specs. 0.5–3.5 mm, 06. 1997 and 1998 outside the Centre Hélio-Marin (0.5–2 m depth).
R. africana is moderately agile. Body shape of adult spec. (2.1 mm l., 0.4 mm h., 0.5 mm w., tail 0.4 mm) elongated oval (Pl. Ie), juveniles droplet-shaped. Notum smooth. Anterior notum end truncate with very small

head lobes. Foot broader than notum, tail broad and rounded. Eyes difficult to discern, of medium size, deep beneath oval, transparent areas. Anus terminal and median, genital pore one third of the body length anterior to it. 3 rounded gill laminae to the right of the anus, two undivided; the middle lamina divided into 3 laminae.

Dark, warm velvet brown on notum and foot, foot sole and the middle of the tail. Head sides and notum rear lighter brown, viscera dark brown. A dark oval eye-patch bordered opaque white to yellowish on both sides of the head (Pl. If; Pl. IIm part I), reaching into the mantle furrow. Two narrow, opaque white to yellowish cross-bands on the notum: the one on the head straight, the posterior one forming a concave curve towards the notum rear; both bordered by elongated oval, blackish-brown blotches. Sides of the tail transparent, gills brown. Colour varieties. As also described by Cervera *et*

al. (1991) the coloration of our specimens is very variable. The eye patches may be absent (Pl. Ie). The opaque white cross-band on the head may be very weak and the posterior one may be absent. On the notum rear the distribution of dark brown, opaque white and black are very variable, too. We sometimes found very small animals of droplet shape that had a brown notum with a lighter margin, a lighter foot sole and a discontinuous opaque white cross-band behind the large eyes. We assume these to be juveniles of *R. africana*.

Anatomy: Reverse side of jaws (Pl Ve) a triangular field (60 µm l., spec. 0.9 mm) of saucer-shaped scales and buttons; 11 plates, each with 1-4 thunderbolt shaped, thick and short processes, the innermost largest and of equal length (6 µm), the outermost the shortest (2 µm) and again of equal length.

Radula: 31 × 1.1.1 (rad. l. 260 µm, spec. fix. 2.5 mm). Rachidians (17 µm b., sides 10 µm l. and 3 µm h.; Pl. V b,c) bicuspidate with 12-20 dense, fine, finger-shaped, parallel denticles (0.5 µm l.) on each flat cusp, forming a weak arc. A very narrow central depression with a short, pointed and thin, seldom finger-shaped central denticle. Due to this narrow depression these teeth most probably have been mistaken for unicuspidate with light microscopy (Pruvot-Fol 1953). Laterals (base 17 µm l., cusps 18 µm h.; Pl V d) smooth, blunt and sickle-shaped, bases with a pronounced hump of 6 µm h.

4 triangular gizzard plates (100 µm l, spec. 1.9 mm) with 1 × 6, 2 × 7, 1 × 8 lamellae with 3 tips each. Basal beam leaves half to two third of the lamellae free. Male copulatory organ (spermatophore: pl. I/1e) similar to the one of *R. ferruginea* described by Kress (1985 b). No shell detectable by NaOH maceration or in histological sections.

Discussion. Our specimens correspond with some of those from the Strait of Gibraltar redescribed by Cervera *et al.* (1991) as *R. africana*. Meanwhile, especially those of our animals with eye-patches on the sides of the head (Pl. I f; Pl I m part I) are very similar indeed to Pl. II, fig. 53, of Pruvot-Fol (1953). The light brown sides of the head and the opaque white cross-band behind the eyes may lead to misidentify this species as *R. coronata* in the Mediterranean area. The radular structure, however, is quite different between these two species.

Runcina brenkoae Thompson, 1980 (Pl. VIa-c, Table I; Pl. IIk, IIIa,b, Ig/part I)

J moll Stud 46: 154-157, fig. 1 c; locus typicus: Red Island (San Andrea), Rovinj, Yugoslavia, Adria. (Ref.: *Runcina brenkoae* Thompson & Brodie, 1988).
Material: Banyuls: 2 specs. 0.9, 2.1 mm, Sept. 1986; 52 spec. 0.5–3 mm, 1995-1998 from various materials outside the Observatoire and the Centre Hélio-Marin; and from le Racou to Cap l'Abeille at 0.5-10 m depth.
The adult *R. brenkoae* are moderately agile, juveniles are very quick creepers. Body shape of adults (1–3 mm) oval (Pl. IIk, IIIa/part I). Notum smooth, tapered and notched anteriorly without head lobes, and distinctly raised at the rear. Foot as wide as notum, tail long and pointed. Eyes medium-sized, visible often only from the sides. Anus just to the right of the median, common genital orifice one third anterior to it. Three rounded gill laminae (Pl Ig/part I, spec. fix. 1.2 mm l.) to the right of the anus, the middle one subdivided into two laminae; the other two undivided. Juveniles (0.5–1 mm) droplet-shaped, pointed at the mouth, broadest and highest at the posterior notal region (Pl. IIIb/part I)

Ground colour of the body almost transparent whitish fawn to reddish, viscera brownish. Adults with a striking dark brown, black or bordeaux pattern on notum and foot sole: margin lined by an often discontinuous garland (Pl. IIIa/part I), centre with a number of anastomosing longitudinal patches. Notal furrow with very dark patches. Thick opaque white triangular patches pointing at each other on both sides behind the eyes, more white narrowly on the head sides, notal margin and rear, and broadly on the tail sides, here flanking a broad dark median region. Very young animals have first a string of separate dark spots along the notal margin. These spots seem to merge later, thus becoming the garland. Still later dark points appear in the centre of the notum (Pl. IIIb/part I), which finally form anatsomosing patches.

Anatomy: Reverse side of jaws a triangular field (80 × 70 × 46 µm) of bowl-shaped scales; 9 plates with 4-5 pointed prongs each.

Radula (Pl. VIa,b) of two animals of 1.6 mm and 2.1 mm l. identically 27 × 1.1.1 (170 µm length). The smaller of the bilobed rachidians with up to 10 diverging, blunt denticles on each *Cardium*-shaped cusp (0.5 µm l.) forming an arc. Central depression particularly deep and broad, rarely a short, triangular and pointed central denticle. Beneath it there is a striking hump. Sides very long, remarkably diverging and moderately high, and halfway tilted slightly inwards. Laterals smooth, blunt and swan-necked (Pl. VIa,b).

4 gizzard plates, size differing distinctly in two animals of about 2 mm l.: 4 × 64 µm and 4 × 120 µm. 9-10 lamellae (pl. II/6 c), a thick longitudinal basal beam leaving one third of the 1-2 tipped lamellae free. Male copulatory organ similar to the one of *R. ferruginea* described by Kress (1985 b). No shell detectable by NaOH maceration or in histological sections.

Discussion. The specimens found by us in Banyuls correspond in all aspects with the material seen by Thompson (1980) and Thompson & Brodie (1988). We provide additional SEM data on radula, jaw and gizzard plates that had not been given by Thompson & Brodie (1988). We assume that the plates with prongs in the jaws of *R. brenkoae* are what Thompson & Brodie (1988) described as "rod like elements with much divided cusps". The shape of the rachidians is unique among the investigated species because of the extraordinarily broad central depression and the extremely long sides.

Runcina ferruginea Kress, 1977 (Pl. Ia, VId-h, Table I; Pl. If, IIn/part I)

J mar biol Ass UK 57: 201-211, Pl. II, fig. 1-4; locus typicus: Plymouth (Great Britain)
Runcina zavodniki Thompson, 1980: 155–157, fig. 1d (see Thompson & Brodie 1988). (Ref.: Ortea & Urgorri 1981: 149-150, fig. 1 A; Ballesteros & Ortea 1981:
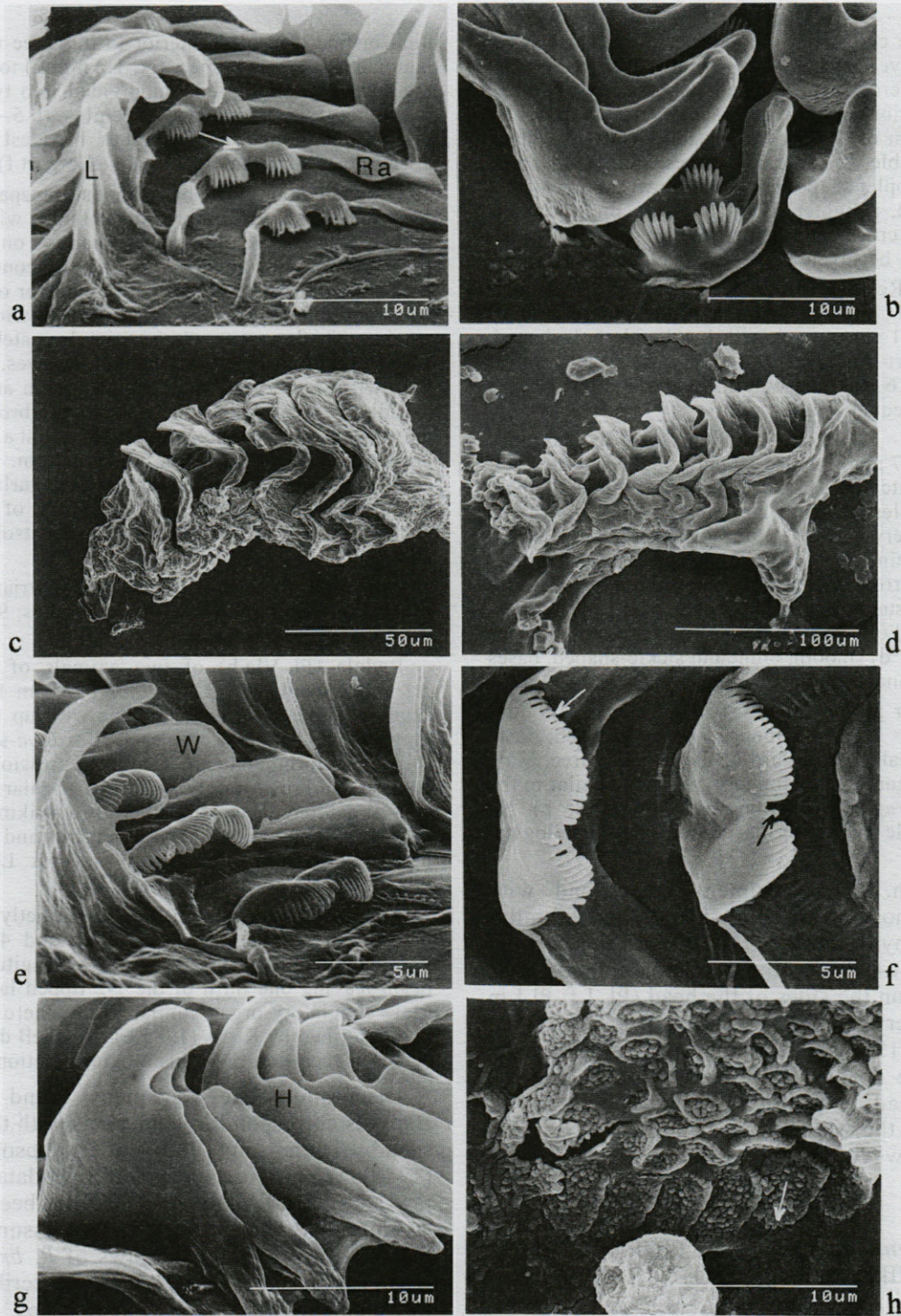
Plate VI. – **a – c**. SEM micrographs of *Runcina brenkoae* Thompson, 1980. **a**, lateral (L) and rachidian (Ra) teeth; arrow: hump; **b**, lateral and rachidian teeth; **c**, gizzard plate. **d – h**. Scanning electron micrographs of *R. ferruginea* Kress, 1977. **d**, gizzard plate; **e**, radula; W wings of rachidian teeth; **f**, rachidian teeth; black arrow: central denticle, white arrow: denticles running very far down the sides of the pads; **g**, lateral teeth; H hump; **h**, part of jaws, reverse side; note plates almost lacking prongs (arrow).

fig. 1A, p. 34; Kress 1985 a, b; Kress 1986; Kress & Schmekel 1992; Kress, Schmekel & Nott 1994).
Material: Banyuls: 4 spec. 1.5–2.1 mm, 03. 1997: Cap Oullestreil 25 m depth, from dived Coralligène; Plymouth: 4 spec. fix. 2–5 mm, 1974/1975, Kress (coll.).

R. ferruginea from Banyuls (2.1 mm l., 0.8 mm w., 0.5 mm h., tail 0.6 mm) is a slow creeper and rests often motionless. Body shape elongated rectangular with small head lobes, notum smooth, anterior border notched, rear rounded and not raised. Eyes of average size,

moderately close to the anterior border. Foot slightly broader than notum; tail long and rounded. Anus median, common genital orifice one third of the body length anterior to it. Three gill leaflets, subdivided horizontally into rounded laminae, to the right of the anus (spec. 3 mm from Plymouth). The most ventral is the largest and most divided one (Pl. Ia; Pl IIf,n/part I).

Our 4 specimens are identical in colour (Pl IIn/part I): notum, foot and tail all over cadmium-orange, viscera dark brown. Entire animal covered with very fine brown specks, somewhat more concentrated along the margins of notum and foot, thus forming a fine brown line. No trace of opaque white on the animal.

Anatomy of two Banyuls specs.: Reverse side of jaws with a triangular field of saucer-shaped scales, and a row of 7 larger rectangular plates (6×4 µm) with 7 very short processes each (Pl. VIh).

Radula: $24 \times 1.1.1$ (150 µm l.; 1 mm spec., Pl. VIe). Rachidian teeth (19 µm w., sides 13 µm l.; Kress (1977): $25 \times 1.1.1$; rach. 12 µm w.) bilobed, with 14-16 fine and parallel denticles of equal length (0.4 µm l.) on each pad, forming an arc with a steep slope mediadly, but less pronounced laterally, running very far down onto the sides (Pl. VIf). Small central depression with finger-shaped central denticle, often strong – sometimes worn down. Sides relatively short and high (pl. II/6e). Laterals (base 14 µm l., cusp 13 µm h.) smooth, blunt and sickle-shaped, base very high with a hump (8 µm h.; Pl. VIg).

4 gizzard plates (90 µm l.); 1×8, 3×7 lamellae with 1-2 tips each. Basal beam low, leaving two third of the lamellae free (Pl. VId). No shell detectable by NaOH maceration or in histological sections.

Discussion. Our material resembles very closely *R. ferruginea* in body shape, coloration and radula, though the colour is more orange than the brownish one described by Kress (1977). A characteristic feature of both is the complete lack of opaque white pigment. Ortea & Urgorri (1981) identified one specimen as *R. ferruginea*. However, there are a few differences: the notum has small, round "rugosites", and the tail is described as more pointed than in the type. The body shape of *R. zavodniki* Thompson, 1980, from Rovinj, according to Thompson & Brodie (1988, fig. 1C), is very similar to *R. ferruginea*. The colour of *R. zavodniki* is jet black all over, but may range over red-brown to pale orange-brown. The radula has denticulate rachidians and smooth laterals, like that of *R. ferruginea* (Pl. IVe, g). Thus we consider these two species to be conspecific (compare Gosliner 1990, p. 145).

Diagnostic features of the world's species of *Runcinacea* except our new species

Ildica nana Bergh, 1889; Mauritius, never rediscovered; blackish or black, notal sides lighter; foot transparent; radula 1.1.1; rach. broad plate with 1 denticle on either side; lat. smooth; external shell.

Ilbia ilbi Burn, 1963 (see Burn 1969); Victoria, Australia; pale purple with a pattern of yellow patches; radula 1.1.1; rach. tricuspidate; lat. denticulate, bifid.

Ilbia mariana Hoff & Carlson, 1990; Mariana Islands; body cream with a middorsal dark area; variable patterns in dark brown, yellow and red; radula 1.1.(1).1; assymmetrical: presumable rach. with serrate central cusp and 4 simple denticles; lat. with denticles.

Metaruncina setoensis (Baba, 1954) (see Ghiselin 1963, Baba 1967); Kii, Middle Japan; blackish, yellowish submarginal band around the notum; foot sole dirty yellowish with minute brown spots; radula 1.1.1, degraded; internal shell.

Pseudoilbia lineata Miller & Rudman, 1968; North Island, New Zealand; notum wrinkled transversely; body speckled with black in five longitudinal bands; each notum end translucent; radula 2.0.2; lat. assymmetrically triangular with a large apical denticle and smaller ones on each side.

Runcinella zelandica Odhner, 1924 (see Willan 1981); North Island of New Zealand; fulvous, sides of foot paler yellowish (fixated animals); radula 1.1.1.1.1; rach. broad, bilobed and denticulated; lat. smooth with one cusp, marginal smooth with 2 cusps.

Runcinella thompsoni Ortea & Rodríguez, 1993; Genovesa Island, Galapagos; dark red, a yellow spot on either side of the head, centre of notum blackish; radula 1.1.1.1.1; rach. bilobed and denticulated; lat. conical, marginal triangular with a thickened cutting edge; large internal, flexible shell.

Runcinida elioti Baba, 1937 (see Baba 1967); Oniike; Japan; back dark brown, yellowish green towards the margins, foot yellowish green; radula 1.1.1; rach. bilobed and denticulated; lat. smooth, hamate.

Runnica katipoides Miller & Rudman, 1968; North Island of New Zealand; dark grey speckled with reddish brown, a dorsal lanceolate, clear central area, flanked by two blackish lines; a white spot above the shell; radula 1.1.1; rach. bilobed and denticulate; lat. triangular with one fine denticle; internal shell.

Runcina adriatica Thompson, 1980; Rovinj, Yugoslavia; yellowish covered with many isolated, round to oval, black patches except on the tail sides; a broad, opaque white cross band behind the eyes, notum rear and tail sides opaque white; radula 1.1.1; rach. bilobed and denticulated; lat. short, hook-shaped, smooth.

Runcina africana Pruvot-Fol, 1953; Témara, Morocco/Senegal; dark brown, head sides and notum rear lighter brown, tail sides transparent, colourless, head sides with dark, oval eye-patches, bordered opaque white; an opaque white to yellowish,

straight cross band behind the eyes, another curved one anterior to the notum rear, both bordered with black patches; colour pattern very variable; radula 1.1.1; rach. bilobed and finely denticulated; lat. swan-necked, smooth.

Runcina aurata Garçía, López, Luque & Cervera, 1986 (Gosliner 1990, Cervera *et al.* 1991); Cádiz, Spain; brownish with dorsal dark patches, interspersed with white-golden specks, a dorsal clear curved band behind the eyes, another on the notum rear; foot greyish, median of tail dark, bordered white; radula 1.1.1; rach. bilobed and denticulated, one denticle bigger; lat. hook-shaped and denticulated.

Runcina australis Burn, 1963; Victoria, Australia; greenish-black; foot and mantle margins and a triangular area over the shell ashy-yellow; radula 1.1.1; rach. bilobed and denticulated; lat. swannecked, finely denticulated; internal shell.

Runcina bahiensis Cervera, Garçía-Gomez & Garçía, 1991; Punta del Rinconcillo, Strait of Gibraltar; notum with small protuberances; light ocre to greenish, with very dense, whitish-ocre pigmentation, except on the edges of notum and foot and the whole foot sole, where there are some small black spots instead; radula 1.1.1; rach. very small and denticulated; lat. hooked and smooth.

Runcina brenkoae Thompson, 1980; Rovinj, Yugoslavia; transparent whitish fawn, covered with anastomosing blackish or dark red patches; head sides behind the eyes with triangular, opaque white patches; notum rear and tail sides opaque white; radula 1.1.1; rach. bilobed, denticulated; lat. swan-necked, smooth.

Runcina capreensis Mazzarelli, 1894; 80 m depth, Capri, Italy, never rediscovered; charcoal black with many irregular big black patches and many small white spots; foot sole yellowish; triangular field of black dots on median of the tail; radula 1.1.1; rach. unicuspidate with one small denticle on each side; lat. hooked and smooth.

Runcina calaritana Colosi, 1915; Golfo di Gagliari, Italy; yellowish-brownish to almost black in the centre of notum and foot, all margins pale yellow or white, enlarged at head sides, notum rear and tail; young animals and larvae with a violet sheen; radula 1.1.1; rach. bilobed, probably denticulated, lat. triangular, probably denticulated.

Runcina coronata (Quatrefages,1844), Bretagne, France; dark brown with very fine yellowish sprinkling, anterior and posterior notal end and head sides broadly bordered cadmium yellow; an curved, opaque white cross band behind the eyes, another anterior to the notum rear. Foot sole and tail yellowish, tail with a dark brown median part; radula 1.1.1; rach. bilobed, irregularily denticulated; lat. triangular, denticulated.

Ildica divae du Bois-Reymond-Marcus & Marcus, 1963, syn. *Lapinura divae* Marcus & du Bois-Reymond Marcus, 1970, *Runcina divae* Clark, 1984; Lesser Antilles; brown all over, notal furrow lighter; radula 1.1.1; rach. denticulated; lat. smooth hooks; adults with external veliger shell.

Runcina falciforme Ortea, Rodríguez & Valdés, 1990; Cabo Verde; notum green with brilliant green, white or blue points on the notum rear; foot green or brown; radula 1.1.1; rach. bilobed and denticulated; lat. denticulated hooks.

Runcina ferruginea Kress, 1977; Plymouth, Great Britain; reddish brown all over, without opaque white; radula 1.1.1; rach. bilobed, denticulated; lat. sickle-shaped, smooth.

Runcina fijiensis Thompson & Brodie, 1988; Fiji; pale yellow with longitudinal black stripes on mantle and upper foot uniting smoothly at the rear; ventral surfaces of mantle and foot without stripes; radula 1.1.1; rach. bilobed with faint denticles; lat. smooth hooks.

Runcina inconspicua Verrill, 1901/02; Castle Harbor, Bermudas, never rediscovered; margins of broad foot thinly undulated; body dark green-brown, small orange margins; upper foot light green with white dots and orange-violet margins.

Runcina lenticula Gofas, Ortea & Rodríguez, 1991; Namibe, Angola; notum chestnut, darker toward the centre; foot and sides of body green; radula 1.1.1; rach. unicuspidate, arched with one single central denticle; lat. smooth (?), sickle-shaped.

Runcina macfarlandi Gosliner, 1991; Oregon, USA; notum yellowish-brown, darker in the centre; eyes only visible from the sides; radula 1.1.1; rach. bilobed and denticulated; lat smooth, elongated, curved.

Runcina macrodenticulata Garçía, Garçía-Gómez & López, 1990; Playa de Benitez, Strait of Gibraltar; brownish or olive green, with dorsal rich dark patches and white specks; head with brown median band, bordered by a longitudinal dark olive green band, and a yellowish white one; median of tail dark olive green; radula 1.1.1; rach. bilobed with irregular denticles; lat. hook-shaped with 8 big denticles

Runcina marshae Burn, 1966; Fiji; dull orange (fixed); eyes visible; radula 1.1.1 rach. denticulated; lat. smooth; internal shell.

Runcina ornata (Quatrefages, 1844) (Ballesteros & Ortea 1981, Garçía *et al.*1986, Cervera *et al.* 1991); Bretagne, France, Eastern Atlantic (1843); Quatref.: similar to *R. coronata*, but generally darker, tail transparent; Garçía *et al.*: blackish with whitish head sides, sometimes joining to an arch behind the eyes; notum rear assymmetrically whit-

ish only on the right side, median of tail blackish; radula 1.1.1; rach. bilobed, with irregular denticles; lat. hooked or triangular and denticulated.

Runcina paupera Ortea, Rodríguez & Valdés, 1990; Cabo Verde; olive greenish with central small black notal spots, clear green notal and foot margins with a yellowish rim; eyes visible; radula 1.1.1; rach. bilobed and denticulated with a straight edge; lat. denticulated (?) hooks.

Runcina prasina (Mörch, 1863); Ste. Croix Island, Antilles, never rediscovered; notum with dense, minute warts and a trilobate rear, notum "prasinum", foot yellowish-green.

Runcina zavodniki Thompson, 1980 (Thompson & Brodie, 1988, comp. description of *R. ferruginea* in the present article); jet black, red brown or pale orange brown all over, no white; radula 1.1.1; rach. bilobed and denticulated; lat. smooth hooks.

Appendix: During the printing process of this article we received two publications with the descriptions of another four new species of *Runcina*, which differ sufficiently from all new species described here in both exterior and interior characters to seperate them without doubt. The summarized descriptions are to be added to the above list.

Runcina gentiana Ortea & Nicieza, 1999; La Gomera, Canary Islands; gentian blue, narrowly bordered with pale blue along the head sides and notum rear; foot violet, tail lighter; radula 1.1.1; rach. bilobed with massive denticles; lat. denticulated.

Runcina hidalgoensis Ortea & Moro, 1999; Teneriffe, Canary Islands and Azores; various shades of rose-red to dark red; radula 1.1.1; rach. bilobed, denticulated; lat. denticulated.

Runcina medanensis Ortea & Moro, 1999; Teneriffe, Canary Islands; uniformly fairly dark red, tail lighter; radula 1.1.1; rach. bilobed with thick denticles; lat. denticulated.

Runcina palominoi Ortea & Moro, 1999; Lanzarote, Canary Islands; red with paired, lateral opaque white patches at the head front, behind the head and in front of the notum rear; sides of the granate red tail white; radula 1.1.1; rach. unicuspidate without denticles; lat. sickle-shaped, smooth.

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THE SPECIES BODY-SIZE DISTRIBUTION
IN IBERIAN ANTS IS PARAMETER INDEPENDENT

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ANT ASSEMBLAGES
BODY SIZE
IBERIAN PENINSULA
MACROECOLOGY
PARAMETER
SPATIAL SCALING

ABSTRACT. – Macroecology aims to reveal hidden patterns in species-level traits over large spatial scales. One important species characteristic is body size. The parameter used to characterize body size *distributions* (BSD) for *individual* data is the mean of any variable representing – or related to – size, including: body length, body mass, forewing length, wing span or cephalothorax length, depending on the animal group. An appreciable proportion (21%) of the species of Iberian ants with workers show varying degrees of different body size (due to polymorphism or by highly variable monomorphism). Taking into account this specific variation in all Iberian BSD, we have explored the effect of a) the range in body size for those variable species, or b) only the maximum attained body size. No effect was detected in either case indicating that the mean dry body mass for *individual* data in Iberian ants, polymorphic species included, is a robust and adequate means of measuring the macroecological patterns of BSD. The mean dry mass for Iberian ants is 0.72 ± 1.01 mg and the median dry mass 0.30 mg (n = 242). For functional studies of local communities it is probably wise to take into account the variable degree of polymorphism.

COMMUNAUTÉS DE FOURMIS
ÉCHELLE SPATIALE
MACROÉCOLOGIE
PARAMÈTRES
PÉNINSULE IBÉRIQUE
TAILLE CORPORELLE

RÉSUMÉ. – La macroécologie, l'étude de la répartition de l'espace physique et des ressources écologiques parmi les espèces, tente de démontrer des patterns dans certains traits spécifiques à des échelles spatiales assez larges. Un trait spécifique très important est la taille corporelle. Pour caractériser la *distribution* spécifique de la masse corporelle, le paramètre utilisé pour les données *individuelles* est la moyenne des variables représentant la taille (longueur du corps, masse, longueur de l'aile antérieure, envergure des ailes, longueur du céphalothorax, selon les différents groupes). Chez les espèces de Fourmis ibériques ayant des ouvrières, une proportion non négligeable (21%) montre un degré de polymorphisme. Ce fait est dû à la présence d'espèces polymorphes et d'espèces monomorphes qui présentent une forte variation. Pour contrôler l'importance de cette variation corporelle nous avons étudié l'influence sur la distribution spécifique de la masse corporelle (matière sèche), a) du rang de variation, et b) du maximum de la masse corporelle atteinte. Aucun effet n'a été détecté ce qui indique que la *moyenne* de la masse corporelle est un paramètre adéquate et robuste pour caractériser les patterns macroécologiques de la taille des Fourmis. La moyenne (± d.s.) des masses corporelles (matière sèche) des Fourmis ibériques est de 0.72 ± 1,01 mg et la médiane 0,30 mg (n = 242). Pour des études fonctionnelles à des échelles locales, il est probablement plus judicieux de tenir compte du polymorphisme.

INTRODUCTION

Macroecological patterns are expected to reveal unapparent properties of how species divide and share physical space and ecological resources (Brown & Maurer 1989, Rosenzweig 1995, Brown 1995). Species-level traits such as body size, geographic range, or abundance, are analysed over large spatial scales and plotted on bivariate plots, sometimes showing strikingly characteristic shapes that call for a biological explanation. Body size is one extremely informative characteristic of any given species (Peters 1983, Calder 1984). The spe-

cies body-size distribution (BSD) of a given group of organisms at different scales has received considerable attention recently. In particular, BSD in local communities tends to be log-uniform (however, see Schoener & Janzen 1968 for an example of the reverse) and is said to turn to log-skewed at the continental scale. This has been shown both for mammals (Brown & Nicoletto 1991, Maurer et al. 1992, Blackburn & Gaston 1994a, also see Bakker & Kelt 2000) and birds (Maurer et al. 1992, Blackburn & Gaston 1994b). The parameter used to characterize body size *distributions* (BSD) for *individual* data is the mean of any variable representing – or related to – size (body length, body mass, forewing length, wing span, cephalothorax length, average for male and female, depending on the animal group) (Blake et al. 1994, Brown & Maurer 1989, Novotny & Kindlmann 1996, Bakker & Kelt 2000). For taxa with a variable adult body size, such as fish, it is not clear which summary statistics should be used (mean, maximum body size) or what its effect is, if any, on the BSD (Blackburn & Gaston 1994b); Brown (1995) observed that a certain measure of variation, such as standard deviation or range of extreme values might also be used.

Ants are a very distinct group in the sense that body size may vary greatly because of polymorphism. This variation has considerable importance in the functioning of ant colonies given that ants of distinct sizes have different functional roles (Hölldobler & Wilson 1990). Therefore, when considering ants, the question of which variable to use when analysing body size distributions is not a trivial issue (nor is it, indeed, for the majority of organisms, in which different stages, from juvenile to adult, are functionally present within the field; however this aspect has not been considered as far as we know). In species of Iberian ants with workers, an appreciable proportion of the species (21%) show variation in body size (due to polymorphism or to highly variable monomorphism). In a recent analysis of Iberian ant sizes (Gómez & Espadaler 2000) the *mean* dry body mass for all species was used, without taking the degree of polymorphism into account. Here we explore the manner in which two distinct variables, specific body size *range* and specific *maximum* size influence the distribution of Iberian ant body sizes at different scales. We have found that mean body size is an adequate and robust parameter for central tendency in analyses of body size distributions even when polymorphic or highly variable monomorphic species are considered. We also explore the effect of body size range and specific maximum size on the relationship between body size and latitude (Cushman et al. 1993) as well as on the BSD, depending on spatial scale (local vs. peninsular) (Brown & Maurer 1989, Blackburn & Gaston 1997).

MATERIAL AND METHODS

Methodological consideration: In a previous study (Gómez & Espadaler 2000) a single formula (Kaspari 1999, Table V, all ants) for deriving biomass was used for the five subfamilies of ants found in Iberia. As four of the five subfamilies of Iberian ants have their own formula –the exception being the Leptanillinae, for which we used the general formula– we used those subfamily formulas to derive new body masses for each species. This consideration applies to all details that follows.

The data base: Using the mean size, the maximum size and taking into account the polymorphism we have generated three data sets of body size distribution for the updated (October 2001) list of 242 Iberian ant species with workers. Workerless parasitic species are not included. Polymorphism was categorized as follows: a) body size classes were stated using a width of 0.3 at a $\log_{10}$ scale (~ 2 mg dry mass); b) for monomorphic species, we used mean body mass, which pertained to a single class; c) for polymorphic species, we used two (minimum, maximum) or three (minimum, mean, maximum) body mass values, which fitted into one, two or three body mass classes, depending on the body mass range. In total, 191 species belonged to one size class, 40 species to two size classes and 11 species encompassed three size classes. Throughout this paper, dry body mass has been analysed, transformed as $\log_{10}$ dry body mass, but has been presented as non-transformed. Means are given ± S.D. Analyses were run under Statistica 5.01 (Statsoft, Inc.; Tulsa, OK) and consisted of pairwise comparisons of different BSD aspects generated when using the three data sets. Means were compared with ANOVA and post-hoc tests when needed, medians with a Kruskall-Wallis test and distributions with a Kolmogorov-Smirnov test. Regression analysis was used to test for a relationship between latitude and mean dry body mass. Bootstrappings were obtained with Simstat for Windows 2.0 (Provalis Research; Montreal, QC).

RESULTS

Peninsular body-size distribution

The frequency distribution of dry masses spans more than three orders of magnitude: the biggest worker ant (*Messor barbarus*, dry mass 16.98 mg) is > 4000 times heavier than the smallest ant (*Leptanilla charonea*, dry mass 0.0038 mg). When using the updated data base of 242 ant species – workerless species not considered–and the specific formulas for each subfamily (Table I) neither the mean dry body mass (ANOVA; $F_{1,482} = 0.14$; $p = 0.70$) nor the median (Mann-Whitney test; $z = 0.14$; $p = 0.88$) were different from those obtained using the general formula for all Formicidae. Nor was the distribution different (Kolmogorov-Smirnov test; max. dif. 0.049; $p > 0.1$) when using the specific or general for-
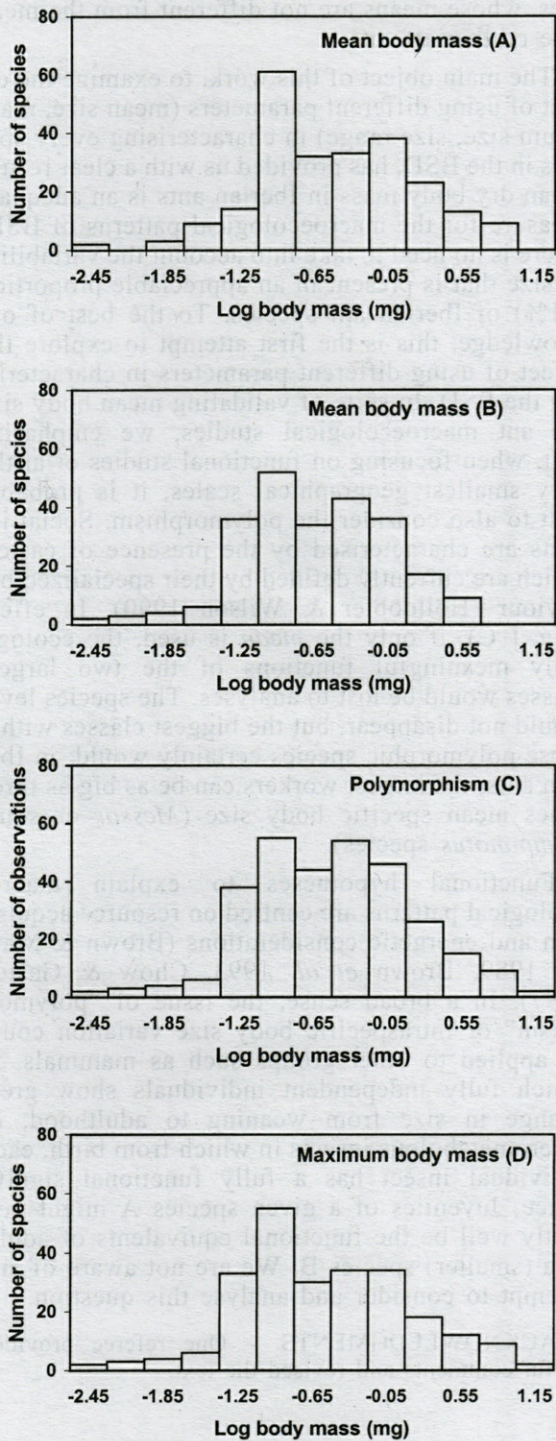
Fig. 1. – Frequency distribution (BSD) of log₁₀ dry body mass of workers of Iberian ant species (n = 242) using different parameters. A: mean, using a single formula to estimate body mass from head length (Kaspari 1999; Table V, All ants). B: mean, using a specific formula for each subfamily (Kaspari1999, Table V but for Formicinae in which we used the formula: *dry mass = 0.4101(head length) 2.6814* (deduced from Espadaler & Gómez 2001). C: using the degree of size variation for polymorphic species (see text); two new bigger classes appear. D: using the upper limit (maximum) of body size.

mula. The body mass of the five subfamilies of Iberian ants was strongly divergent between subfamilies (Table I). We compared each subfamily using two kinds of formulae and the interaction term in ANOVA; no statistical difference ($F_{4,473} = 0.94$; $p = 0.43$) in the mean body mass was detected, neither when the dry body mass was estimated with the formula for each subfamily, nor when it was estimated with a general formula for the family Formicidae. In spite of the absence of statistical differences, in the work that follows we used the BSD generated with the specific subfamily formulas because, even if the difference is minimal, it is still more correct.

Formal tests of normality (Lilliefors & Shapiro-Wilks' W test) were conducted on the three BSD (using the mean, the maximum or polymorphism). Lilliefors test rejected normality in the BSD when using maximum size ($p < 0.01$) and the Shapiro-Wilks' test rejected normality in the BSD using the mean ($p < 0.01$) and the maximum size ($p < 0.02$). Neither test rejected normality in the BSD using polymorphism ($p < 0.15$ and $p < 0.06$).

Variable to characterize body size and local assemblages

Although to the naked eye, certain differences can be seen in the BSD depending on the variable used (mean, polymorphism, maximum; Fig. 1, Table I), there are no statistical differences between the *means* of BSD based on mean body size or on polymorphism (ANOVA, $F_{2,785} = 2.76$; $p = 0.063$), between the *medians* of BSD (Kruskal-Wallis test; $H_{2,788} = 4.6$; $p = 0.09$) or between all *distributions* of BSD (Kolmogorov-Smirnov tests; $p > 0.1$ for all possible pairs of comparisons). A separate comparison of the BSD mean and median for local inventories at the smallest scale (< 10 km^2) and for different localities also failed to show any differences, whether the mean dry body mass or polymorphism were used (Kruskal-Wallis and Kolmogorov-Smirnov tests; $p > 0.1$). These latter results are not presented here.

Local assemblages on Iberian ants

We applied a bootstrapping procedure to test if the local assemblages were a random sub-sample of the entire Iberian BSD or were different in a systematic way, as is usually assumed (Brown & Nicoletto 1991, Gaston & Blackburn 1996, but see Bakker & Kelt 2000). We drew 1000 random sub-samples from the entire Iberian BSD, with the same number of species for a given locality. The proportion of those simulations that were less than the observed median was taken as an indication of the failure to reject the null hypothesis of no difference between the two assemblages: in no case was

Table I. – Top, Dry body mass (mg) of Iberian ants according to subfamily. Different superscripts indicate statistical differences by a post-hoc Tukey's test (unequal n) following ANOVA ($F4$, $237 = 34.4$; $p < 001$). N = species number. Mean dry mass calculated from raw data: 0.72 ± 1.01 mg; median dry mass: 0.30 mg (n = 242). The mean corresponds to *Myrmica wesmaeli*; the median to *Goniomma blanci*. Bottom, dry body mass of Iberian ants using different parameters (mean, maximum, polymorphism) for *individual* data (=species). For the mean and maximum n is the number of species without considering the presence and degree of polymorphism; when polymorphism is considered (see text) some species contribute more than one value to the distribution pushing the data up to 304 values (not species).

Subfamily	Mean ± s.d.	N
Ponerinae	$0.32 \pm 0.26^{a,b}$	10
Myrmicinae	0.49 ± 0.86^{a}	131
Dolichoderinae	0.17 ± 0.08^{a}	10
Formicinae	1.22 ± 1.16^{b}	86
Leptanillinae	0.008 ± 0.003^{c}	5

	Mean ± S.D.	Median	n
Mean	0.72 ± 1.01	0.30	242
Maximum	1.23 ± 2.41	0.34	242
Polymorphism	1.22 ± 2.22	0.43	304

a difference detected, as had already been obtained in Gómez & Espadaler (2000).

Latitudinal trend

This trend was also absent. The mean dry body mass of local samples was not greater at higher latitudes within the Iberian Peninsula (mean dry body mass = $-1.09 + 0.07$ latitude; $r^2 = 0.058$; F = 0.49; p = 0.5).

DISCUSSION

We maintain the same general conclusions as in a previous paper (Gómez & Espadaler 2000): 1) In Iberian ants, the relative body size of the most diverse genus (*Leptothorax*) is 29.2%, well within the range found by Dial & Marzluff (1988), indicating that there is a much higher number of smaller species than of larger ones; 2) Particular subsets of species at the local scale are not different in their BSD from random samples taken from the entire Iberian ant fauna, and do not show a growing log-uniformity at smaller scales. 3) Latitude has no bearing on the mean size of local sam-

ples, whose means are not different from the mean size of Iberian ants.

The main object of this work, to examine the effect of using different parameters (mean size, maximum size, size range) in characterising every species in the BSD, has provided us with a clear result: mean dry body mass in Iberian ants is an adequate measure for the macroecological patterns of BSD. There is no need to take into account the variability of size that is present in an appreciable proportion (21%) of Iberian ant species. To the best of our knowledge, this is the first attempt to explore the effect of using different parameters in characterising the BSD. In spite of validating mean body size for ant macroecological studies, we emphasize that, when focusing on functional studies or at the very smallest geographical scales, it is probably best to also consider the polymorphism. Social insects are characterised by the presence of castes, which are currently defined by their specialized behaviour (Hölldobler & Wilson 1990). In effect (Fig. 1 C), if only the *mean* is used, the ecologically meaningful functions of the two largest classes would be lost to analyses. The species level would not disappear, but the biggest classes within those polymorphic species certainly would: in Iberian ants, the largest workers can be as big as three times mean specific body size (*Messor* or some *Camponotus* species).

Functional hypotheses to explain macroecological patterns are centred on resource acquisition and energetic considerations (Brown & Maurer 1989, Brown *et al.* 1993, Chow & Gaston 1997). In a broad sense, the issue of "polymorphism" or intraspecific body size variation could be applied to other groups such as mammals, in which fully independent individuals show great change in size from weaning to adulthood, or heterometabolous insects in which from birth, each individual insect has a fully functional significance. Juveniles of a given species A might perfectly well be the functional equivalents of adults in a (smaller) species B. We are not aware of any attempt to consider and analyse this question.

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BASE DE DONNÉES
SUR LES COPÉPODES PLANCTONIQUES MARINS

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Le site créé par l'Observatoire Océanologique de Banyuls (Université Pierre et Marie Curie, Paris VI et Institut des Sciences de l'Univers-CNRS) présente diverses contributions des travaux scientifiques réalisés au Laboratoire Arago.

Parmi ces contributions une synthèse sur les Copépodes planctoniques marins des origines à 2000/2001 constitue une référence dans le domaine de la biodiversité.

Etablie après analyse de 3000 articles (faunes, description des espèces, travaux d'écologie et de physiologie), cette synthèse couvre l'ensemble des Océans et des mers du globe.

Pour chacune des espèces les synonymies sont indiquées, ainsi que les références morphologiques (Ref.) et des références complémentaires récentes non exhaustives (Ref. compl.). Les localisations géographiques (Loc.) sont précisées. Le nombre de citations des espèces par les auteurs est noté (N). Les longueurs totales (Lg.) des adultes sont indiquées, avec les auteurs (annexe : auteurs-tailles). Des remarques (Rem.) précisent certaines observations comme la bathymétrie ou les renvois (Cf.) pour les espèces « tombées » en synonymie.

Une matrice résume la distribution des espèces dans 24 zones géographiques.

Ce travail complète et corrige les publications parues dans les *Annales de l'Institut Océanographique*, Paris (Razouls 1995, 1996, Razouls & de Bovée 1998).

Les références bibliographiques complémentaires de celles de Vervoort (in *Crustaceana*, 1986, 1986 a & 1988) indispensables pour toute recherche sur les Copépodes complètent (bien que de manière non exhaustive) le travail de 1986 à 2000/2001.

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Les références bibliographiques complémentaires de celles de Vervoort (in Crustaceana, 1986, 1988 à 1988) indispensables pour toute recherche sur les Copépodes complètent (bien que de manière non exhaustive) le travail de 1985 à 2000-2001.

Tous les documents cités sont présents à la bibliothèque du laboratoire Arago.

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HYPERLINK <http://www.obs-banyuls.fr/zooplancton/copepodes/accueil.htm> Ce travail étant considéré comme relevant de la littérature scientifique se doit d'être cité comme indiqué sur la page web ci-dessus.

VARIATION IN ABUNDANCE AND POPULATION DYNAMICS OF THE SEA-URCHIN *PARACENTROTUS LIVIDUS* ON THE CATALAN COAST (NORTH-WESTERN MEDITERRANEAN SEA) IN RELATION TO HABITAT AND MARINE RESERVE

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SEA-URCHIN
DENSITY
SIZE DISTRIBUTION
MEDITERRANEAN SEA
MARINE RESERVE

ABSTRACT. – We surveyed the population structure of the sea-urchin *Paracentrotus lividus*, considering the impact of depth, habitat and protection on its abundance and size distribution. No difference was found between habitats (walls *vs.* boulders) whereas a depth gradient was highlighted for the abundance and the size distribution of the sea-urchin. Most of the population (about 80%) is located in shallow areas (less than 10 m depth) whatever the location. Shallow water populations were made of small and medium size individuals (< 50 mm in diameter) while deep water populations were made of large individuals (> 50 mm in diameter). These large individuals accounted for 57% of the population in deep areas while they only represented 11% in shallow habitats. Since the recruitment in the deep waters cannot explain the abundance of large individuals, we suggest that larger individuals originate from shallow water populations, migrating to deep habitats while growing. In addition to differences linked to depth, we also observed significant differences between localities, higher abundances of sea-urchin being observed in the marine protected area than outside (193.6 *vs.* 82.5 ind. per 10 m^2). However, rather than a protection effect, such result seems to be the consequence of a lower recruitment outside the protected area as the lower abundance of juveniles was observed out of the protected area. This last observation demonstrates the existence of a micro-geographic variability in the population structure of *Paracentrotus lividus* and much attention should be paid on this aspect prior to test the protection effect.

OURSINS
DENSITÉ
DISTRIBUTION DE TAILLES
MER MÉDITERRANÉE
RÉSERVE MARINE

RÉSUMÉ. – Nous avons décrit une population d'Oursins, *Paracentrotus lividus*, en analysant simultanément l'impact de la profondeur, de la qualité de l'habitat et de la protection sur l'abondance et la distribution des tailles. Les deux habitats sélectionnés pour présenter les plus fortes abondances d'Oursins (parois verticales-roches-blocs), n'ont pas induit de différence significative dans les populations. A l'opposé, nos résultats montrent l'existence d'un gradient d'abondance et de taille avec la profondeur. La majeure partie de la population (80%) se situe dans les zones peu profondes (< 10 m) alors que les individus les plus gros (diamètre > 50 mm) se regroupent dans les zones profondes, en dessous de 10 m. Ils représentent près de 57% de la population dans les strates profondes. Dans la mesure où le recrutement se concentre principalement dans les zones peu profondes, nous proposons que la population profonde soit formée d'individus ayant migré vers ces zones profondes au cours de la croissance. Au delà de ces caractéristiques naturelles des populations, nous avons également constaté une différence significative d'abondance en fonction de la protection avec une moyenne de 82 ind. pour 10 m^2 en zone non protégée contre près de 193 ind. pour 10 m^2 en zone protégée. Néanmoins, il convient de tempérer ce résultat par le fait que les jeunes individus (< 20 mm de diamètre) sont également plus abondants dans le site protégé, ce qui suggère que la différence d'abondance résulte en grande partie d'un recrutement plus important dans le site protégé. Il faudra donc tenir compte de cet aspect pour évaluer l'effet réserve sur les Oursins.

INTRODUCTION

In infralittoral communities of the Western Me-
diterranean, the sea-urchin *Paracentrotus lividus* is
the key species for the control of the dynamics of
seaweeds and seagrasses because of its high abun-
dance compared to other species (Palacin *et al.*
1998). It occurs mostly in shallow waters (maxi-
mum depth 20m), where it can reach densities of up
to 10 individuals per square meter (Harmelin *et al.*
1980, 1981, Verlaque 1987, Palacin *et al.* 1998). In
high densities areas, it can eliminate brown algae
and seagrasses and thereby induce the formation of
a bare patch dominated by encrusting algae (Kempf
1962, Verlaque & Nédelec 1983, Verlaque 1987).

The gastronomic value of its gonads has led to
intensive harvesting with consequent reduction of
populations in some areas along the Mediterranean
coasts of France and Spain (Le Direach *et al.*
1987). Because of their fishery value, the factors
determining the structure of *Paracentrotus lividus*
populations have been investigated, and identifying
mainly the recruitment process (Azzolina 1987,
Lozano *et al.* 1995) and the mortality induced by
predation (Verlaque 1984, Savy 1987) as factors
determining the adult subsequent population. This
predation appeared mostly due to fish such as the
labrid *Coris julis* that is a major predator of juve-
niles (Sala 1997) and sparids like *Diplodus sargus*
and *D. vulgaris* being the main predators of adults
(Garcia-Rubies & Zabala 1990, Garcia-Rubies
1996, Sala 1997). In addition, the intense harvest-
ing focused on sea-urchins has direct effect on
their abundances (Le Direach *et al.* 1987). Never-
theless, fisheries target *Diplodus* species in the
Mediterranean sea that will reduce the natural pre-
dation on sea-urchins and may balance the poten-
tial decrease of sea-urchin populations due to hu-
man collections (Jennings & Kaiser 1998). This
interaction between fisheries and sea urchin high-
lights indirect relationships refereed to trophic cas-
cades (Estes & Palmisano 1974).

Once discussed in the context of marine pro-
tected area, therefore it becomes difficult to predict
the evolution of sea-urchin populations because
they will be protected from collecting but they may
be exposed to more intense natural predation by
fish. Many studies on the Mediterranean rocky lit-
toral have demonstrated that large piscivorous and
invertebrate-feeding fish are more abundant within
marine protected areas compared to no protected
sites (e.g. Bell 1983, Harmelin *et al.* 1995, Vacchi
et al. 1998). In contrast, many studies comparing
abundance and density of sea-urchin populations
show variable results. Sala & Zabala (1996) moni-
tored the abundance of *Paracentrotus lividus*
within and outside the Medes islands marine re-
serve (NE Spain) for three years and reported a pat-
tern of lower abundance in the reserve relative to
nearby unprotected areas. This pattern was attrib-
uted to increased predatory fish abundance in the
reserve (Garcia-Rubies & Zabala 1990). Latter, a
similar survey did not found any significant differ-
ence in density and mean size and conclude that
these last results did not support the cascade hy-
pothesis (Sala *et al.* 1998).

The aims of the present study were to describe
the density and size structure of *Paracentrotus
lividus* populations according to habitats and
depths in some rocky habitats in the north-western
Mediterranean Sea and ultimately to make compar-
isons among protected and unprotected areas using
the Cerbère-Banyuls Marine Reserve as protected
areas.

MATERIAL AND METHODS

Paracentrotus lividus were collected in April 1999 in
the Cerbère-Banyuls Marine Reserve and a nearby un-
protected area (South of France, north-western Mediter-
ranean Sea) (Fig. 1). The study was conducted in 3
localities experiencing similar exposure to wind and wa-
ves but different constraints in terms of protection: the
Totally Protected Area (TPA), the Partially Protected
Area (PPA) and the Unprotected Area (UPA) (Fig. 1). In
the TPA, all human activities are forbidden. In the PPA,
recreational fishing is authorised for both fish and inver-
tebrates as well as professional fisher using only fixed
nets. In the UPA, no constraints are in place except those
concerning spear-fishing and fishing regulations eve-
rywhere. The Cerbère-Banyuls Marine Reserve has been
established in 1974 and spread over 7 km of coastline.
We chose a marine protected area because we want to
avoid the effect of collection on description of the natu-
ral population features. Each of the three localities
(TPA, PPA and UPA) was separated from the other by 3
to 4 km. In each locality, 2 habitats were identified:
"boulder" habitats (we turned them up to inspect under
surfaces) that were colonised by a rich algal assemblage,
and vertical and sub-vertical "walls" that supported
algae as well as other invertebrates. In each habitat, col-
lections were made at two different depths: a shallow
zone between 0 to 10 meters depth, and a deeper zone
between 10 to 20 meters depth.

Abundance and population size structure of sea-ur-
chins were studied by scuba-diving along transects of
10 m long and 1 m wide. Each site was made of three
transects. Altogether the sampling accounted for 36 tran-
sects that were all sampled within a month period (April
1999). The time of sampling took place before the re-
cruitment season (Lopez *et al.* 1998) and therefore we
mostly counted adults and juveniles of the previous year.
For each transect, *Paracentrotus lividus* individuals
were counted and their diameter (test without spines)
was measured to the nearest mm with a calliper. Data
were further grouped in 10 mm size classes.

To test for difference in abundance and mean size
between localities, habitats and depth, a three-way
ANOVA was performed after verifying the homogeneity
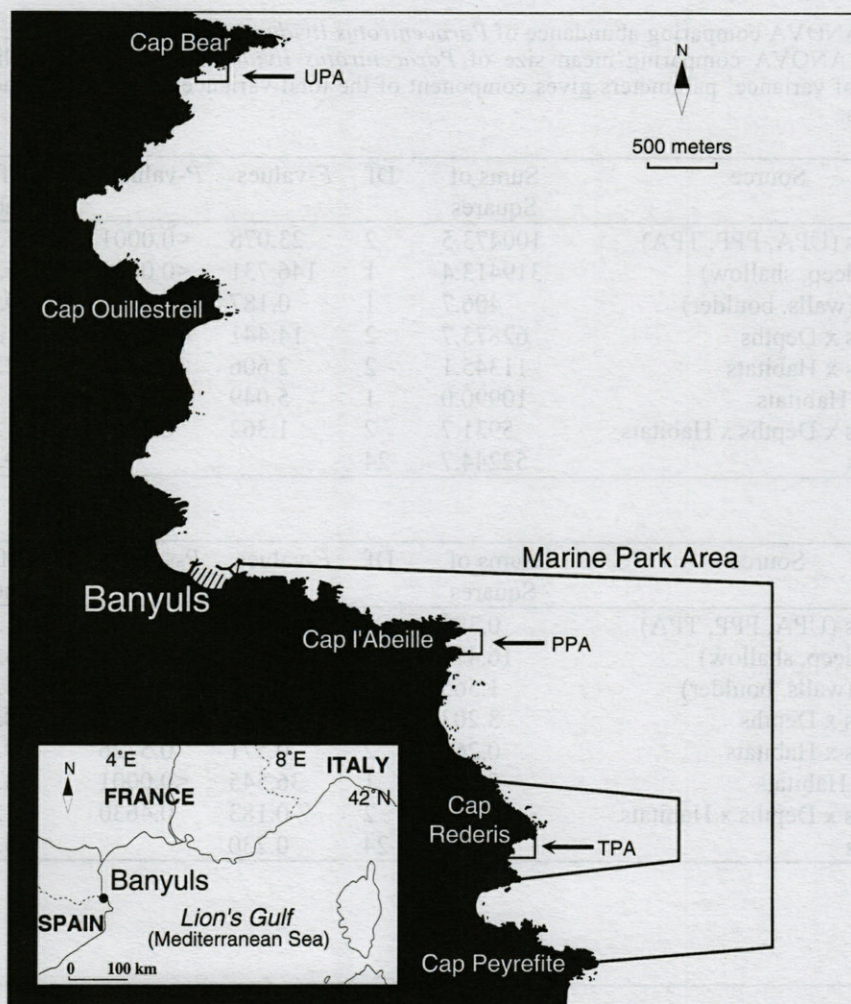of variance and the normality of data (Scherrer 1984).

Fig. 1. – Location of the three areas where sea-urchins were counted according to depths and habitats with replicates of 10 m². UPA = Unprotected area; PPA = Partially protected area and TPA = totally protected area.

RESULTS

Over all transects, we counted and measured a total of 5637 individuals. Abundance of *Paracentrotus lividus* varied from 29 to 517 individuals per transect. In the following sections, we will use abundance values since they can be easily translated into density as each transect represented 10 square meters. Comparisons of abundance of *P. lividus* with a three-way ANOVA (Table I) demonstrated significant difference in the combined factor 'locality × depth' (p < 0.0001) as well as single factors 'locality' (p < 0.0001) and 'depth' (p < 0.0001). Overall, the deeper areas showed continuously lower abundance than shallow ones in all localities (mean abundance = 62.4 *vs.* 250.8 individuals per transect). In addition, localities exhibited significant difference with much lower abundance of urchins in the UPA (mean abundance = 82.5 individuals per transect) compared to PPA and TPA (mean

abundance = 185.3 and 202.0 individuals per transect respectively) (Fig. 2A). Among the three sources showing significant divergence of the abundance, the 'depth' accounted for 67% of the variance while 'locality' and the combined factor 'locality × depth' explained 21 and 13% of the total variance respectively. Abundance did not vary significantly according to the type of habitat, boulders and walls (Fig. 2).

Similar analysis were performed using the mean size of individuals per transect. The size of *Paracentrotus lividus* specimens recorded in this survey varied from 5 to 75 mm. The mean size of individuals collected per transect varied from 20.6 to 60.0 mm. Comparison of mean size of the populations of each transect show significant differences among habitats and depth (Table I). The three-way ANOVA demonstrated significant differences in 4 sources: the single factors 'habitat' (p = 0.015) and 'depth' (p < 0.0001) and the com-

Table I. – Three-way ANOVA comparing abundance of *Paracentrotus lividus* according to localities, depths and habitats (top). Three-way ANOVA comparing mean size of *Paracentrotus lividus* according to localities, depths and habitats (bottom). '% of variance' parameters gives component of the total variance explained by each factor and the combination of factors.

Source	Sums of Squares	Df	*F*-values	*P*-values	% of variance
Localities (UPA, PPP, TPA)	100473.5	2	23.078	<0.0001	17.82
Depths (deep, shallow)	319413.4	1	146.731	<0.0001	56.67
Habitats (walls, boulder)	406.7	1	0.187	0.6694	0.07
Localities x Depths	62873.7	2	14.441	<0.0001	11.15
Localities x Habitats	11345.1	2	2.606	0.0946	2.01
Depths x Habitats	10990.0	1	5.049	0.0341	1.95
Localities x Depths x Habitats	5931.7	2	1.362	0.2751	1.05
Residuals	52244.7	24			9.27

Source	Sums of Squares	Df	*F*-values	*P*-values	% of variance
Localities (UPA, PPP, TPA)	0.391	2	0.848	0.4409	1.08
Depths (deep, shallow)	16.411	1	71.197	<0.0001	45.39
Habitats (walls, boulder)	1.565	1	6.790	0.0155	4.33
Localities x Depths	3.203	2	6.948	0.0042	8.86
Localities x Habitats	0.263	2	0.571	0.5726	0.73
Depths x Habitats	8.424	1	36.545	<0.0001	23.30
Localities x Depths x Habitats	0.367	2	0.183	0.4630	1.02
Residuals	5.532	24	0.230		15.29
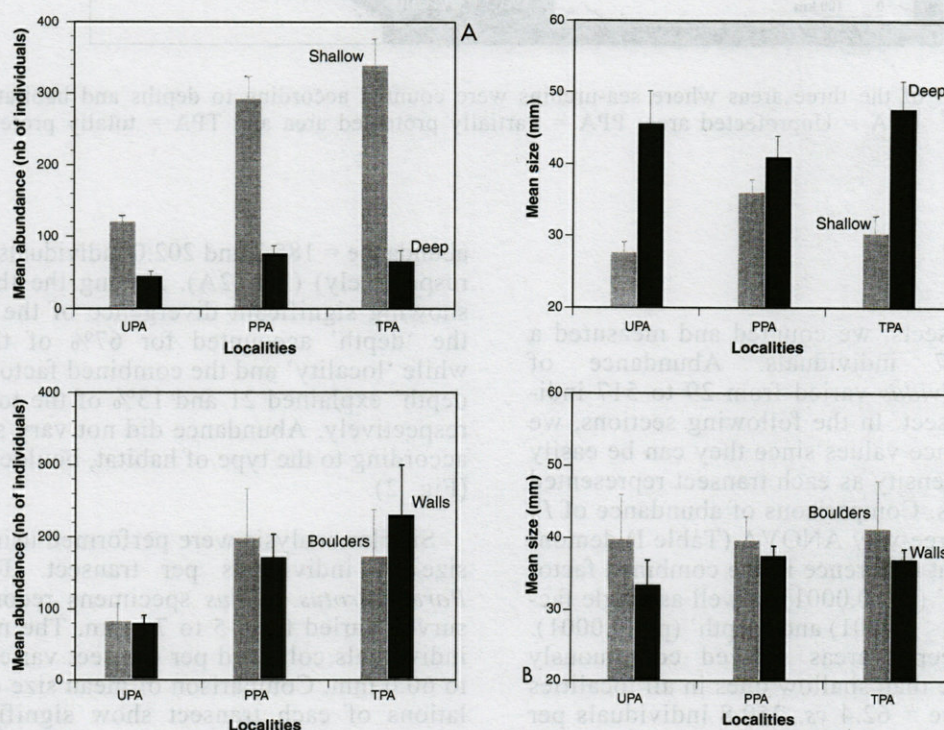
Fig. 2. – A, Mean abundance per transect of 10 m² according to depth (top) and habitats (bottom), considering each locality. B, Mean size (mm) of individuals counted in each transect according to depth (top) and habitats (bottom), considering each locality. Error bars give standard error.
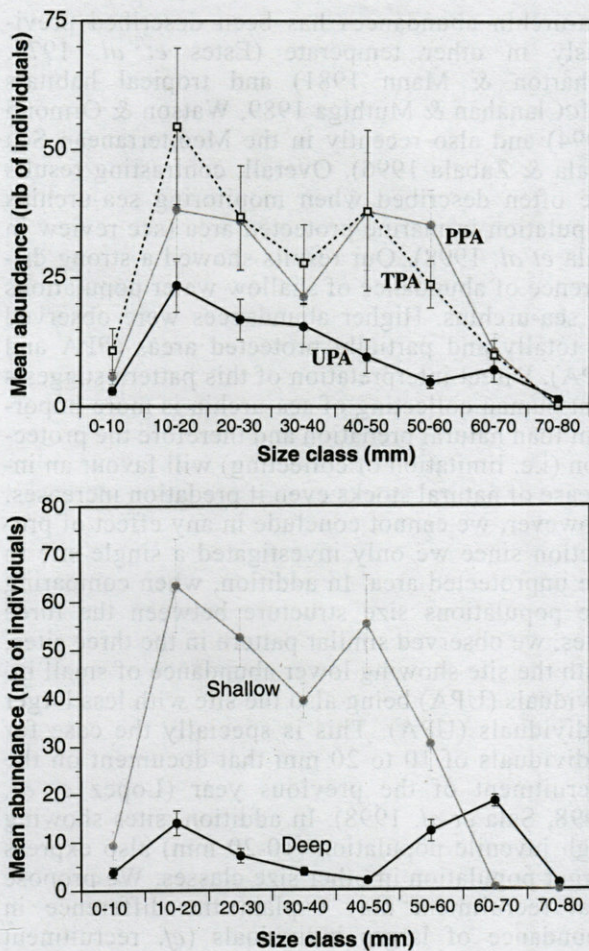
Fig. 3. – Top, Mean abundance for each size class and considering separately each locality whatever depth and habitat. Bottom, Mean abundance for each size class, considering separately each depth whatever locality and habitat. Error bars give standard error.

bined sources 'locality × depth' (p = 0.004) and 'habitat × depth' (p < 0.0001). Overall, these significant differences come from individuals that are much smaller in shallow areas (31.3 vs. 44.8 mm in deeper areas) and walls (36.0 vs. 40.2 mm in boulders), both whatever the locality (Fig. 2B). The depth explained most of the variance (45%) while the habitat only accounted for 4%. Mean sizes were similar between localities (Fig. 2B).

Finally, we detailed the size distribution looking at variations between localities, habitats and depth. Regarding localities, the lower value of abundance found in UPA compared to the other sites (PPA and TPA) was consistent in all size classes except for large individuals (Fig. 3). The three localities showed similar distribution pattern, small individuals (10 to 20 mm in diameter) being the most abundant. Among the 8 single-factor ANOVA computed for each size class between localities, only the 50-60 mm size class showed significant differ-

ence (p = 0.006) mostly because this size class was under-represented in the UPA samples. The size class of recruit of the previous year (10 to 20 mm) show also significant difference between localities (p = 0.01) with UPA population being less abundant than the two others (PPA and TPA). The size classes distribution varied significantly according to depth. As previously observed, most of the population was located in the shallow transects and only large individuals (50 to 70 mm in diameter) were more abundant in the deeper habitats (Fig. 3). After exclusion from the data, the very small individuals that were not targeted in our sampling design (lower than 10 mm diameter), shallow habitats showed a decrease of individuals as they become larger. Deeper habitats showed similar decrease in smaller through to medium size classes but larger individuals became the most abundant size class. Larger individuals (> 50 mm diameter) accounted for 57% of the population in the deeper habitats while they only represented 11% in the shallow habitats. Among the 8 single-factor ANOVA computed for each size class among the depth distribution, all size classes exceeding 20 mm diameter differed significantly between shallow and deep habitats. Finally the size class distribution did not differed according to the habitat structure (boulder vs. walls).

DISCUSSION

Overall, our results demonstrated significant differences in abundance and size distribution of *Paracentrotus lividus* according to localities and depths but not depending on substrates. Differences among localities and depth appeared highly significant, and little affected by micro-geographic variation since the variance among transects within the same site only accounted for 15 and 9% of the total variance in abundance and size respectively (see the residuals in three-way ANOVA, Table I).

The recruits of the year are smaller than 10 mm and often appear to be the most numerous in the population (Lopez *et al.* 1998, Barnes *et al.* 1999). In the present work, this size class is one of the less abundant because our sampling protocol did not include total cleaning of some surface and observation under binocular. Therefore, analysis of this class is not representative of the recruitment. The upper size class (10-20 mm) appears to be the most abundant in shallow waters (and almost in deeper waters). Individuals belonging to this size class are assumed to be recruits of the previous year like suggested by Lopez *et al.* (1998) and Sala *et al.* (1998). Our data showed that they preferentially occurred in shallow waters, whatever the habitats considered. This difference, according to depth range, can result from variation in the number of recruits settling at each depth, or from a differen-

tial predation on a similar number of recruits. The main predator of juveniles *P. lividus* in the north-western Mediterranean Sea is *Coris Julis* (Sala 1997). Previous fish survey in the same areas where we prospected for sea-urchin populations did not show significant differences in density of *C. Julis* (Dufour *et al*. 1995). Therefore, the difference according to depth in the recruits density mainly result from recruitment processes in shallow waters (Lopez *et al*. 1998). However, a differential abundance of predators other than *C. julis* (fishes or invertebrates) may also contribute to enhance this difference.

The difference in density between shallow and deep areas remains stable in all small and medium size classes including all individuals smaller than 50 mm in diameter. Larger individuals (> 50 mm in diameter) were equally distributed between shallow (31.8 ind. per 10 m²) and deeper (30.7 ind. per 10 m²) areas. Such similarity in population density of large individuals is opposed to the strong divergence found in smaller individuals and can result from migration of larger individuals to deeper habitats or from higher predation on large individuals in shallow habitats. Major predators of adults *Paracentrotus lividus* and *Diplodus sargus* and *D. vulgaris* (Sala 1997), which occur uniformly between the surface and 20 meters depth (Dufour *et al*. 1995, Jouvenel 1997) and cannot explain the shift in density of sea-urchins. In addition to natural predation, we must also consider that human collection which is significant in the Mediterranean Sea would be more intense in shallow water (Palacin *et al*. 1998). However, in our survey we found more large individuals in deep water than small ones at the same depth (average of 31.8 large individuals vs. 30.6 small ind.). Therefore, the recruitment itself, in deep habitats, cannot explain the abundance of large individuals and some migrations have also contributed to the deeper populations. The human collection will contribute to decrease the shallow populations but this decrease is also due to migration of larger individuals into deeper habitats. This migration was already described in sea-urchins and more specifically in *Paracentrotus lividus* (Dance 1987, Crook *et al*. 2000, Barnes & Crook 2001). Such change in habitats will be linked to change in feeding and other biological features that is still to be investigate.

Our data also revealed significant difference in population density between the three sites surveyed. The three sites varied mostly in their protection status. Protection usually leads to increases of density, biomass, diversity and/or longevity of populations experiencing fishing pressure (Polunin & Roberts 1993, Roberts 1995). Regarding sea-urchin populations, reserve effect is more complex to estimate since it is necessary to integrate "cascade effect" (Francour 1989, Sala & Zabala 1996). The relationship between predator (fish or human) and

sea-urchin abundances has been described previously in other temperate (Estes *et al*. 1978, Wharton & Mann 1981) and tropical habitats (McClanahan & Muthiga 1989, Watson & Ormond 1994) and also recently in the Mediterranean Sea (Sala & Zabala 1996). Overall, contrasting results are often described when monitoring sea-urchins population in marine protected area (see review in Sala *et al*. 1998). Our results showed a strong difference of abundance of shallow water populations of sea-urchins. Higher abundances were observed in totally and partially protected areas (PPA and TPA). Direct interpretation of this pattern suggests that human collecting of sea-urchin is more important than natural predation and therefore the protection (i.e. limitation of collecting) will favour an increase of natural stocks even if predation increases. However, we cannot conclude in any effect of protection since we only investigated a single site in the unprotected area. In addition, when comparing the populations size structure between the three sites, we observed similar pattern in the three sites, with the site showing lower abundance of small individuals (UPA) being also the site with less larger individuals (UPA). This is specially the case for individuals of 10 to 20 mm that document on the recruitment of the previous year (Lopez *et al*. 1998, Sala *et al*. 1998). In addition, sites showing high juvenile population (10-20 mm) also express larger population in other size classes. We propose that recruitment may explain the difference in abundance of larger individuals (*cf*. recruitment limitation theory). Finally, the variation in abundance seems to result from variation in recruitment between sites rather than any effect of predation or collecting.

Our results have been analysed in term of recruitment, fish predation and human predation. These are not the only perspectives in understanding spatial variation in population structure. Behavioural aspects have been also emphasised in sea-urchins (Barnes & Crook 2001). However, this study highlights micro-geographic variations in the abundance of the population while the habitat does not seem to affect this difference. Micro-geographic variations in the distribution of marine organisms are now been observed in many surveys dealing both with population dynamics and population genetics (David *et al*. 1997, Lenfant & Planes 2002). Such aspect needs now to be considered while looking at any scale survey and when looking at the impact of some specific aspect such as the effect of protection.

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INSTRUCTIONS AUX AUTEURS

TEXTE

Les manuscrits, dactylographiés en double interligne sur le recto seulement des feuilles numérotées (ne pas excéder 20 pages) sont présentés en trois jeux complets, sous leur forme définitive.

Le titre du manuscrit doit être le plus court possible; il est suivi du prénom et du nom de l'auteur (ou de chacun des auteurs) ainsi que de l'adresse (ou des adresses) du Laboratoire dans lequel a été effectué le travail.

Chaque manuscrit comportera :
— un résumé en français de 15 lignes maximum figurant en début d'article, suivi de sa traduction en anglais,
— des mots clés en français et anglais (6 au maximum) permettant un traitement rapide par des revues analytiques,
— un titre abrégé pour haut de page (60 signes et espaces au plus),
— la traduction anglaise du titre de l'article,
— une liste hors-texte des légendes des illustrations et leur traduction en anglais,
— une liste hors-texte des légendes des tableaux numérotés en chiffres romains et traduites en anglais.

Les noms scientifiques (genres, espèces, sous-espèces) figurent en italiques ou soulignés d'un seul trait.

Les références bibliographiques des auteurs cités dans le texte sont regroupées à la fin du manuscrit dans l'ordre alphabétique des noms d'auteurs; elles doivent être conformes aux modèles suivants :

Park GS, Park SY 2000. Long-term trends and temporal heterogeneity of water quality in tidally mixed estuarine waters. *Mar Poll Bull* 40 (12): 1201-1209.

Edvardsen B, Paasche E 1998. Bloom dynamics and physiology of *Prymnesium* and *Chrysochromulina*. *In* Anderson DM, Cembella AD & Hallegraeff GM eds, The Physiological Ecology of Harmful Algal Blooms. Springer Verlag, Heidelberg: 193-208.

Le titre des périodiques doit être abrégé d'après les règles internationales (World list of Scientific Periodicals).

Les notes infrapaginales et les remerciements seront aussi brefs que possibles.

ILLUSTRATIONS

Les figures au trait doivent être exécutées à l'encre de chine sur papier calque assez fort, bristol, carte à gratter, papier millimétré bleu. Il est exigé des lettres et chiffres « transfert » par caractères autocollants pour le lettrage et la numérotation, dont la taille tient compte de la réduction à supporter. Les figures sont regroupées au maximum en planches dont la justification pleine page est de 17 × 24,35 cm une fois réduites (penser à retrancher la légende de ces dimensions); largeur d'une colonne : 8,1 cm. Méthode des « rectangles homologues » pour la réduction : tracer les diagonales d'un rectangle de 17/24,35 cm, les prolonger; tout rectangle admettant ces prolongements comme diagonales correspondra à la justification après réduction. Indiquer le numéro d'ordre des figures en chiffres arabes et le nom de l'auteur au crayon bleu au recto ou au dos. Ne pas inscrire de légende sur les illustrations.

Regrouper les similis (photographies, lavis...) en planches. Employer une échelle graphique qui sera réduite avec la figure, et un lettrage par transfert. Tableaux et planches similis numérotés de 1 à N en chiffres romains. Limiter le nombre des tableaux et ne retenir que ceux qui sont indispensables à la compréhension du travail.

La revue publie gratuitement 2 planches au trait pleine page et 1 seule planche en simili; les illustrations supplémentaires ou en couleurs sont facturées aux auteurs.

ÉPREUVES ET TIRÉS À PART

Un jeu d'épreuves accompagné du manuscrit est envoyé à l'auteur qui doit retourner l'ensemble après correction et indication de la place des illustrations dans le texte, dans un délai maximum de 15 jours.

Les tirages à part, facturés directement par l'imprimeur, doivent être commandés dès réception de l'imprimé spécial joint aux épreuves.

INSTRUCTIONS TO AUTHORS

TEXT

The manuscript should be typed double-spaced on one side of white paper, format A4, pages numbered (max. 20 pp), and sent in definitive form, in triplicate, to the editor.

The title of the paper should be as concise as possible; it is followed by the first and second name of the author(s) and address of the laboratory at which the work was done.

Each manuscript should include:
— a french summary of 15 lines max., followed by the english translation,
— key words in french and english (6 max.) allowing treatment by abstracting journals,
— short version of title (60 signs and spaces max.),
— english translation of the full title,
— a separate list of figure legends in english and french,
— a separate list of numbered tables with their legends in english and scientific names (genera, species, sub-species) should be written in italics or underlined once.

References of papers cited in the text should be listed at the end of the manuscript in alphabetical order, according to the following models:

Park GS, Park SY 2000. Long-term trends and temporal heterogeneity of water quality in tidally mixed estuarine waters. *Mar Poll Bull* 40 (12): 1201-1209.

Edvardsen B, Paasche E 1998. Bloom dynamics and physiology of *Prymnesium* and *Chrysochromulina*. *In* Anderson DM, Cembella AD & Hallegraeff GM eds, The Physiological Ecology of Harmful Algal Blooms. Springer Verlag, Heidelberg: 193-208.

The title of a journal must be abbreviated according to the rules set by the World list of Scientific Periodicals.

Footnotes and acknowledgments should be as brief as possible.

ILLUSTRATIONS

Line drawings should be prepared with India ink on heavy tracing paper, bristol board, white drawing-cardboard or graph paper (blue grid). Letters and numbers on figures should be large enough to be easily readable after reduction; use letter transfer equipment. As far as possible, figures should be grouped in plates of 17 × 24.35 cm final size (generally the explanations are included in this frame); the width of a single column is 8.1 cm. Prepare figures using the "homologous rectangles" rule; indicate the number of the figure and the author's name with blue pencil on the back of the figure. Do not write explanations on the figure.

Photographs and half-tone drawings must always be grouped as plates. Scale bars are reduced with the figures. Number plates and tables in roman numbers on the back. Limit total number of tables to an absolute minimum of items indispensable for clear presentation.

The journal publishes free of charge two plates with line drawings and one plate of half-tone figures per article. Additional illustrations and colour plates are charged to the author(s)

GALLEY-PROOFS AND REPRINTS

One set of galley-proofs is sent with the manuscript to the author(s); both proofs and manuscript must be returned to the editor with indications on indispensable corrections and insertion of figures within two weeks.

Reprints can be ordered by using the form enclosed with the galley-proofs.

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