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ELECTROPHORETIC HETEROGENEITY IN *HEDISTE DIVERSICOLOR* (ANNELIDA: POLYCHAETA) WITHIN AND BETWEEN ESTUARIES IN NORTHERN FRANCE

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SOLUBLE PROTEINS
TWO-DIMENSIONAL ELECTROPHORESIS
ESTERASES
NEREIDIDAE
ESTUARIES
HEDISTE DIVERSICOLOR

ABSTRACT. – We compared the general protein and non-specific esterases band patterns of different populations of the polychaete annelid *Hediste diversicolor* (O.F. Müller) (Nereididae) located at different spatial scales in the estuaries of Aa, Canche, Authie and Rance (France). Our results indicate a restricted gene flow between populations located in different estuaries but also within the same estuaries. These results could be explained by the particular life cycle of this species (“benthopelagic” life cycle with a brief semi-pelagic larval phase) which does not favour a great dispersion of larvae and by local marine currents and eroding channels which canalize an oriented dissemination of larvae. In a preliminary step, intra-population banding pattern variability was assessed in two populations by high resolution two-dimensional electrophoresis analysis of proteins. Our results show a great inter-individual variability in protein profiles. These results are in good concordance with the hypothesis of the existence of a restricted gene flow between populations.

PROTÉINES SOLUBLES
ELECTROPHORÈSE BIDIMENSIONNELLE
ESTÉRASES
NEREIDIDAE
ESTUAIRES
HEDISTE DIVERSICOLOR

RÉSUMÉ. – Nous avons comparé les profils électrophorétiques des protéines générales et des estérases non-spécifiques de différentes populations de l'Annélide Polychète *Hediste diversicolor* (O.F. Müller) (Nereididae) localisées à différentes échelles d'espace dans les estuaires de l'Aa, de la Canche, de l'Authie et de la Rance (France). Nos résultats indiquent un flux génétique restreint entre les populations localisées dans les différents estuaires ainsi qu'à l'intérieur même des estuaires. Ces résultats pourraient être expliqués par la nature particulière du cycle de vie de cette espèce (cycle « benthopélagique » avec une phase larvaire semi-pélagique brève) qui ne favorise pas la dispersion des larves ainsi que par les courants marins locaux et les chenaux d'irrigation qui canalisent une dissémination orientée des larves. Lors d'une étape préliminaire, la variabilité intra-population des profils électrophorétiques de deux populations a été appréciée après analyse par électrophorèse bidimensionnelle hautement résolutive des protéines. Nos résultats montrent une grande variabilité inter-individuelle des profils électrophorétiques et sont en parfait accord avec l'hypothèse selon laquelle il existerait un flux génétique restreint entre les populations.

INTRODUCTION

Among nereidid polychaetes, *Hediste diversicolor* (O.F. Müller, 1776) (= *Nereis diversicolor*) is a wide-spread species in the intertidal zone of marine and brackish waters throughout Europe. Its range extends from the Baltic sea to Morocco and the Mediterranean, Black and (by introduction) Caspian Seas (Fauvel 1923, Clay 1967, Smith 1977). Moreover, *H. diversicolor* is a constant species of the *Macoma baltica* community and occurs in all

European estuaries. This species is able to tolerate great variations of temperature (Ivleva 1970, Wolff 1973) and salinity (Wolff 1973, Neuhoﬀ 1979) and to survive to drastic conditions of hypoxia (Wells & Dales 1951, Kristensen 1983). As a consequence, *H. diversicolor* is able to settle in naturally-fluctuant environments such as the upper waters of estuaries. *H. diversicolor* is an infaunal species which inhabits sandy muds but also gravels, clays and even turf (Rullier 1959, Amanieux 1967, Clay 1967, Cazaux 1970, Elkaim 1974, Desprez 1981, Bachelet 1987) where it builds U or

Y-shape burrows (Lambert & Retière 1987). According to Goerke (1971) and Fauchald & Jumars (1979), this species is omnivorous. Its individual feeding behaviour consists of two different strategies, one in which mucous is secreted to collect food particles as a pellet form at the opening of the burrow and the other without mucous secretion but direct food ingestion (Esnault *et al.* 1990).

H. diversicolor populations are conspicuous elements of benthos in intertidal mudflats and estuaries; they form an important part of the food supply for various birds and bottom-dwelling fishes. This species is a potentially valuable organism for long-term monitoring programs and as a bioindicator (Scaps 1997, Scaps & Borot 2000) and is also used commercially as a bait (Scaps 1992, Olive 1994, Gambi *et al.* 1994). So, it is of prime importance to characterize populations within and between estuaries.

Some authors have studied genetic differentiation in shallow brackish-water polychaetes of the family Nereididae. Abbiati & Maltagliati (1992) have showed that two populations of *Neanthes succinea* from the Tyrrhenian Sea and the Adriatic Sea are reproductively isolated. Fong & Garthwaite (1994) have compared biochemically using ten allozyme loci three morphologically similar species of the polychaete genus *Hediste* [*H. limnicola*, *H. diversicolor* and *H. japonica*] respectively from the west coast of North America, Europe and Japan. These authors have found that these three taxa are genetically distinct and constitute valid species. *H. limnicola* recognized previously as a self-fertilizing hermaphrodite is quite polymorphic in the four populations examined and these authors suggest that cross-fertilization must occur in the field. More recently, Sato & Masuda (1997) have demonstrated genetic differentiation in two sibling species of the polychaete *Hediste japonica*. Concerning *H. diversicolor*, previous studies have showed allozyme evidence of genetic differentiation between populations from the North Sea and the Baltic Sea (Röhner *et al.* 1997) and from the Western Mediterranean (Abbiati & Maltagliati 1996). Moreover, some authors have found a substantial degree of genetic differentiation between estuaries (Hateley *et al.* 1992, Fong & Garthwaite 1994).

In order to study the relationships between genetic structure and mode of reproduction and dispersal, we compared the general protein band and non-specific esterase band patterns of different populations of *H. diversicolor* located at different spatial scales in four estuaries along the English Channel and the North Sea. The general protein band and non-specific esterase band patterns, can be produced relatively easily and used for direct comparison of different populations of *H. diversicolor*. Moreover, in order to assess intra-population banding pattern variability, high resolution two-dimensional electrophoresis analysis of proteins was performed.

MATERIALS AND METHODS

Collection of individuals and sampling sites: individuals were collected by hand in a restricted area from different localities of North France during Spring of 1998 (28 April to 17 May). Individuals were obtained from 13 sites located along the estuaries of Aa, Canche, Authie and Rance. The sampling sites are shown in figure 1 and their related habitats described in Table I. These estuaries are located along the English Channel and the North Sea. Thirty individuals were collected per site.

Only one sample was collected on the northern side of the Aa estuary near the beach of Grand-Fort-Philippe, 6 stations were sampled along the Canche estuary on the northern and the southern sides. At station 3, a transect was designed and 3 samples collected along this transect. Sites 3a, 3b and 3c correspond respectively to a stagnant pool located at the upper tidal level, an eroding channel located at mid-tide level and an isolated pool located at the lower tidal level. In a similar manner, another transect was designed on the southern side of the Authie estuary near the mouth. Sites a, b and c correspond to samples collected within an isolated pool located at the upper tidal level and in an eroding channel at the mid-tide level, and at the lower tidal level respectively. The last sample was collected onto the mudflat of La Richardais immediately located above the tidal power station of the Rance estuary.

Sample preparation: worms were kept alive in an aquarium at 15 °C, continuously supplied with natural sea water and aeration. Worms were used for preparing samples within a period of two days following the collection.

Assays in polyacrylamide gradient gel electrophoresis were performed on pooled extracts proceeding from 30 individuals. Animals were homogenized at 4 °C into 4 volumes of ice-cold 0.01 M Tris/HCl, pH 8.0 and then centrifuged at 15 000 g for 30 min at 4 °C. The supernatant was used for the electrophoretic analysis.

In order to analyze abundant proteins of adults by two-dimensional electrophoresis, four adults were sampled from the Aa and the Authie estuaries (site b). The preparation of samples for two-dimensional electrophoresis was carried out on excised metamereres. We used the method described by Boyer *et al.* (1993) with minor modifications for the preparation of samples. Metamereres were reduced into a powder directly in liquid N₂ using a mortar and a pestle. One ml of extraction solution (10% w/v trichloroacetic acid, 0.07% v/v β -mercaptoethanol in cold acetone) was added. Proteins were precipitated at -20 °C for 45 min. After centrifugation at 30 000 $\times$ g for 20 min at 4 °C the supernatant was discarded and the pellet washed twice with 1 ml β -mercaptoethanol (0.07% v/v) in cold acetone at -20 °C for 45 min, in order to remove any residual TCA. After centrifugation at 30 000 $\times$ g for 20 min at 4 °C, the β -mercaptoethanol solution was discarded and the pellet dried for at least 2 hours. To solubilize the proteins, the pellet was resuspended for 2 h in a lysis buffer (Damerval *et al.* 1986) (60 ml/mg dry weight pellet) and then centrifuged at 30 000 $\times$ g for 20 min at 4 °C. Supernatants were stored at -70 °C for further analysis.

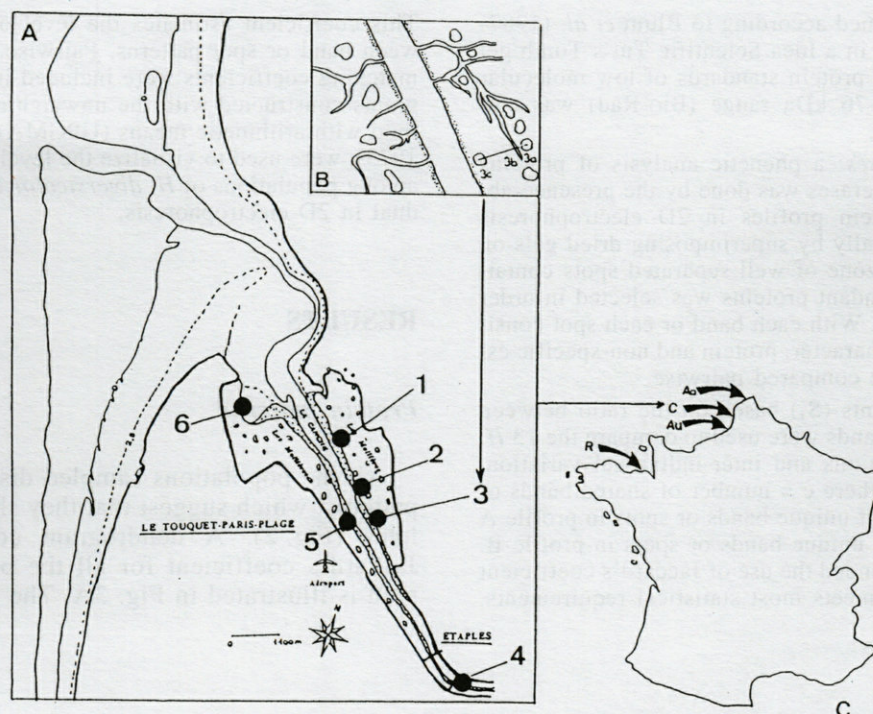


Fig. 1. – A, Sampling sites in the Canche estuary. B, Detail of the transect at station 3. C, Map of France with geographical location of Aa, Canche (C), Authie (Au) and Rance (R) estuaries.
See Table I for details of site numbering.

Table I. – Description of sampling sites.

Code	Site	Sediment type
Canche estuary sites		
1	Military cemetery	Soft mud
2	La Pinède camping site	Soft mud
3a	Les Mollières	
	Upper tidal-level	Compact soft mud
3b	Mid tidal-level	Very soft mud
3c	Lower tidal-level	Soft mud
4	Etaples	Muddy sand
5	Le Touquet airport	Soft mud
6	Le Touquet nautical circle	Sandy mud
Other sites		
Aa	Aa estuary	Soft mud with some pebbles and debris (e.g. cans, fragments of bottles,...)
a	Mouth of Authie estuary	
	Upper tidal-level	Soft mud
b	Mid tidal-level	Soft mud
c	Lower tidal-level	Very soft mud
R	Rance estuary	Organically rich mud

Electrophoretic analysis:

Polyacrylamide Gradient Gel Electrophoresis (PAGGE): Polyacrylamide gradient gel electrophoresis (PAGGE) under non-denaturing conditions was performed on a 5-30% acrylamide gel as described by Scaps *et*

al. (1996). Migration was carried out at 4 °C for the appropriate period of time necessary to obtain a stabilized protein pattern, i. e. 20 to 22 hours. After being separated by electrophoresis, protein were stained with a 0.1% solution (w/v) of brilliant blue Coomassie isopropanol-acetic acid-water (2.5/1/6.5). Gels were washed with a 10% solution (v/v) of acetic acid. Gels were also stained for non-specific esterases (EST; EC 3.1.1) according to the method of Selander *et al.* (1971).

Two-dimensional electrophoresis (2D-PAGE): two-dimensional electrophoresis was essentially performed as described by O'Farrell (1975) with the modification of Hilbert *et al.* (1992) using the Protean II cell (Bio-Rad, Richmond, CA). Isoelectric focusing gels utilizing diacrylylpiperazine as the cross-linking agent in place of bisacrylamide were prepared. Ampholytes were added to a final concentration of 5.5% and consisted of 90% ampholytes (pH 3-10) and 10% ampholytes (pH 5-7). About 100 mg of protein were loaded on the basic end of the capillary tubes. The gels were 1 mm in diameter and 13.5 cm long. The isoelectric focusing (IEF) was performed at room temperature with a constant voltage of 1 200 V for 17.5 h, followed by 1 500 V for 0.5 h and power was limited to 3 W. IEF capillary gels were extruded from the glass tubes, equilibrated and loaded onto a 12% homogeneous SDS gel. Gels were electrophoresed in the running buffer (24 mM Tris base; 192 mM glycine; 0.1% SDS). Electrophoresis in the second dimension was carried out with a constant voltage of 350 V until the dye front reaches the bottom of the gel (approximately 3 h).

After electrophoresis, gels were fixed overnight in 200 ml of a solution containing 50% ethanol, 12% glacial acetic acid and 200 µl 35% formaldehyde. Silver

staining was performed according to Blum *et al.* (1987) and gels were dried in a Idea Scientific Tut's Tomb gel dryer. A mixture of protein standards of low molecular weight in the 17.5-76 kDa range (Bio-Rad) was employed as reference.

Statistical analyses: a phenetic analysis of proteins and non-specific esterases was done by the presence-absence criteria. Protein profiles in 2D electrophoresis were evaluated visually by superimposing dried gels on a bench viewer. A zone of well separated spots containing about 250 abundant proteins was selected in order to compare the gels. With each band or each spot considered as a distinct character, protein and non-specific esterase patterns were compared pairwise.

Jaccard coefficients (S_J) based on the ratio between shared and unique bands were used to compare the 13 *H. diversicolor* populations and inter-individual variation. $S_J = c/a_u + b_u + c$ where c = number of shared bands or spots, a_u = number of unique bands or spots in profile A and b_u = number of unique bands or spots in profile B. Shi (1993) recommended the use of Jaccard's coefficient because this index meets most statistical requirements.

This coefficient estimates the level of divergence between band or spot patterns. Pairwise data of Jaccard's matching coefficients were included in matrix. Dendrograms constructed with the unweighted pair group method with arithmetic means (UPGMA) (Sneath & Sokal 1973), were used to visualize the level of differentiation among populations of *H. diversicolor* and among individual in 2D electrophoresis.

RESULTS

Protein patterns

All the populations sampled displayed common patterns, which suggest that they share common alleles (Fig. 2). A dendrogram constructed from Jaccard's coefficient for all the populations sampled is illustrated in Fig. 3A. The two populations

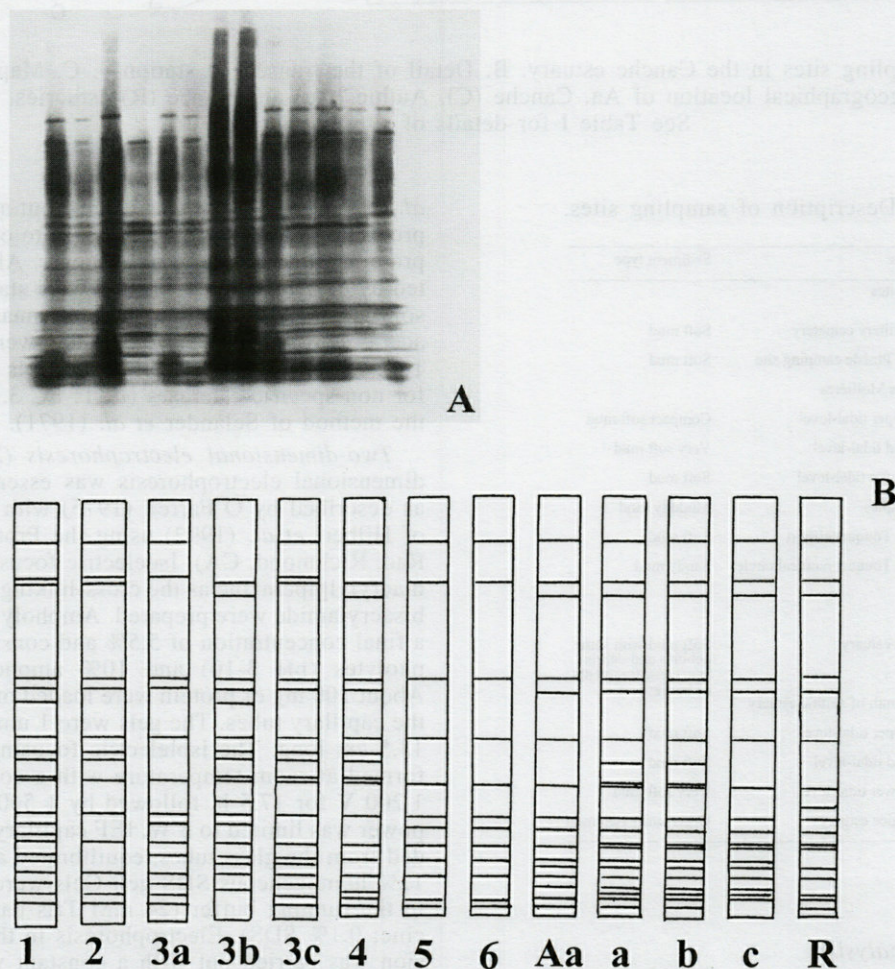
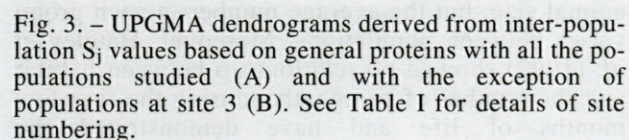


Fig. 2. – PAGGE profiles of general proteins in *Hediste diversicolor* from 13 sites located along the estuaries of Aa, Canche, Authie and Rance (A). Interpretation of general protein profiles (B), not same scale. See Table I for details of site numbering.

If we suppress populations 3a and 3c which are located in very isolated pools and population 3b which is situated at a higher tidal level than the other populations in the Canche estuary, we still do not observe clear clustering of populations (Fig. 3B).

All the sampled populations shared the same common bands (Fig. 4). A dendrogram constructed from Jaccard's coefficient for all the populations sampled is illustrated in figure 5A. As for general protein patterns, the two populations from the southern side of the Canche estuary (5 and 6) and the two populations sampled within the irrigation channel of the Authie estuary (site 8) but from two different tidal levels (a and b) have similar patterns ($S_j = 1$). There is also no apparent correlation between S_j and the geographic distance; in fact, the more distant population (R) is not opposite to the other populations.

If we suppress populations at site 3, we observe a clear discrimination between populations located in different estuaries (Fig. 5B). Moreover, there is an opposition between populations located on the northern (1, 2) and the southern (5, 6) sides of the Canche estuary which cluster differently. Population 4 which is more distant from the mouth of the estuary than the other populations located on the northern side of the Canche estuary cluster with the populations of the southern side.



In a preliminary step, the general protein pattern of four individuals from the Aa estuary and four individuals from the Authie estuary (site a) were compared by 2D-PAGE in order to assess inter and intra-population variation.

An example of 2D-gel pattern is presented in Fig 6. Using high resolution two-dimensional electrophoresis, we have separated more than 1 000 protein spots. Spots were observed over most of the molecular weight and pH ranges used. We selected about 100 spots located in the best resolution region of the gels in order to compare intra and inter-individual variability (Fig. 6). The overall pattern of the gels were similar enough to permit direct comparisons and identification of persistent polypeptides (Fig. 7).

A dendrogram constructed from Jaccard's coefficient is illustrated in figure 8. We observe a clustering of individuals from the Authie estuary. Individuals from the Aa estuary cluster but in two different groups and are separated from the individuals of the Authie estuary; this means that inter-individual variability in protein profiles in 2D-PAGE is very high.

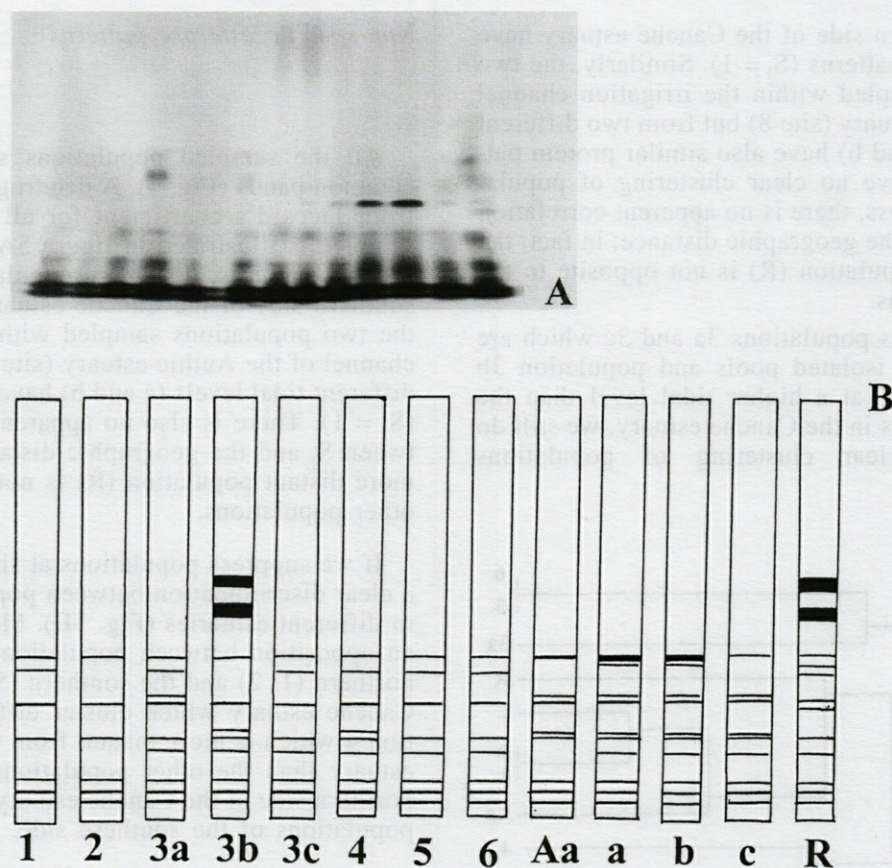


Fig. 4. – PAGGE profiles of esterases in *Hediste diversicolor* from 13 sites located along the estuaries of Aa, Canche, Authie and Rance (A). Interpretation of general protein profiles (B), different scale. See Table I for details of site numbering.

DISCUSSION

Population divergence at different geographical scales

As samples are separated by an average distance of about ten meters, hundred of meters, kilometers and hundred of kilometers, it is possible to test hypotheses relating to the relative contribution of migration in the population genetic differentiation. We have shown for the non-specific esterase and the protein patterns of *H. diversicolor* that bands are shared by all the sampled populations suggesting the monospecificity of this species. In the case of high level of gene flow maintaining genetic similarity, we would predict that interlocality differences over the largest scale of geography would be the greatest. Results obtained from both the general proteins and the non-specific esterases show that the population of the Rance estuary is not more distant from the other populations which are, at a closer geographical scale. So, our results indicate that the gene flow is restricted also at a relatively small scale. However, d'Hondt & Goyffon (1986)

noticed that protein patterns are not informative enough to study the genetic variability between populations.

Previous studies on the reproductive strategy of the polychaete *H. diversicolor* over its geographical range has revealed differences in the spawning season and the age of maturity (Table II). Inter-population physiological differences have also been noticed by Hateley *et al.* (1992). The offspring from Tvarminne (Finland) develop more easily at a lower salinity than those from Kristineberg (Sweden). Differences in degree of metal tolerance have also been observed between populations within a single small estuary (Grant *et al.* 1989). Similarly, inter-population morphological differences have also been reported (Barnes 1978, Barnes & Head 1977, Gillet 1986, 1990, Hateley *et al.* 1992, Khlebovich *et al.* 1982, Muus 1967a and b, Varriale 1973, Vignocchi 1981). The number of paragnaths showed no relationship with animal size, but the average number in each group varies between populations. Moreover, Hateley *et al.* (1992) showed no relationship between habitat and the number of paragnaths, during the first few months of life and have demonstrated the

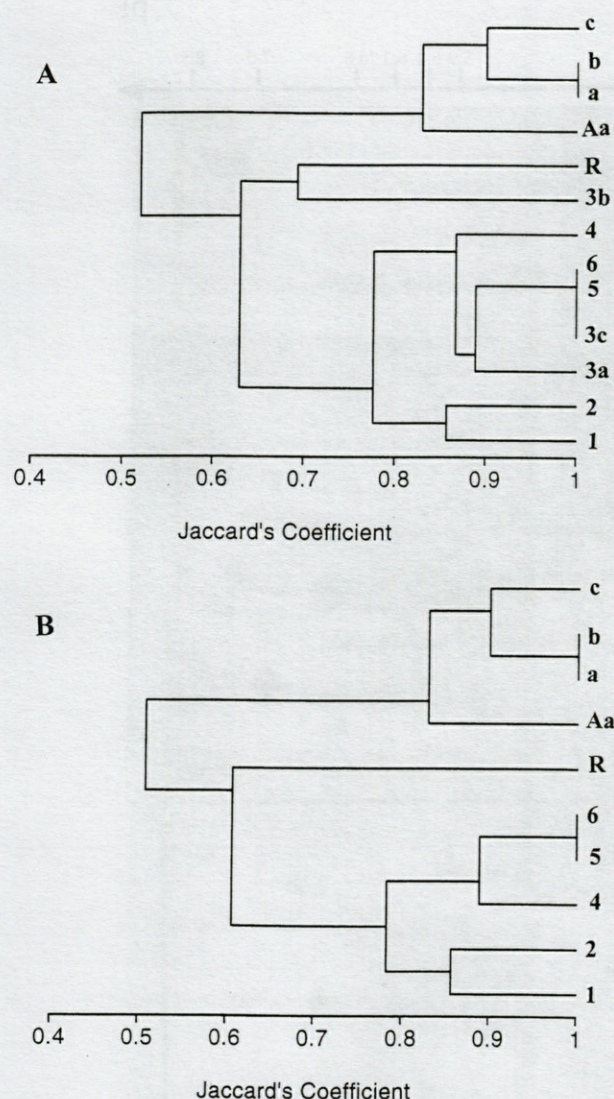


Fig. 5. – UPGMA dendrograms derived from inter-population S_j values based on esterases with all the populations studied (A) and with the exception of populations at site 3 (B). See Table I for details of site numbering.

heritability of the paragnath number by cross-fertilization experiments at least for four of six size groups. However, these authors pointed out that causes for this inter-population paragnath variation are not clear. It is possible that the paragnath number reflects differences in diet or the dominant mode of feeding. The mechanical implications of these methods for paragnaths are likely to be different. Differences in salinity tolerance of larvae (Smith 1964) and in time of reproduction may be entirely explained by plastic responses towards fluctuating environments (Hateley *et al.* 1992, Scaps 1992). Recently, allozyme evidence of genetic differentiation between populations of *H. diversicolor* from the North Sea and the Baltic Sea

(Röhner *et al.* 1997) and from the Western Mediterranean (Abbiati & Maltagliati, 1996) was demonstrated.

Our results suggest that there is a substantial genetic heterogeneity between estuaries. According to Hateley *et al.* (1992) the differences in paragnath number between populations and patterns of variation in allozymes at two loci are consistent with a substantial degree of genetic differentiation between estuaries. Moreover, Fong & Garthwaite (1994) have examined populations of *H. diversicolor* which were separated by about 30 km, and suggested that observed differences could be explained either by a restricted gene flow between populations or short-term selection.

Microgeographic variation

Genetic heterogeneity will be discussed on a small spatial-scale, within estuaries and at different levels of the intertidal zone.

Estuarine variation

Our results showed no differentiation in the two populations sampled on the southern side of the Canche estuary. In contrast, inter-populations differences appeared between populations sampled on the northern side of the same estuary although they are located at the same intertidal height (populations 1, 2, and 4). Population 4 is distant from the mouth of the estuary and the channel at this site is narrow; in consequence, this population behaves as a population of the southern side. These results suggest the existence of a basic population heterogeneity within the Canche estuary. It is useful for the following discussion to describe the life cycle of *H. diversicolor*. According to Cazaux (1970), *H. diversicolor* has a "benthopelagic" life cycle with a brief semi-pelagic phase. Eggs are large (egg diameter = 300 μ m), lecithotrophic, demersal and, according to experimental observations (Bartels-Hardège & Zeeck 1990) are laid by the female inside the burrow before the male ejects its sperm into the burrow's entrance. The female subsequently intensifies its ventilatory activity and brings back the sperm into the burrow in a kind of feeding behaviour. Fertilized eggs remain into the maternal burrow, to be brooded by the female. Hatching occurs at the trochophore stage. Larvae exhibit a slightly developed ciliary crown and often crawl on the bottom or remain in the maternal burrow until reaching the 7 or 8 segments stage. Then the female dies. At the end of the "semi-pelagic" phase, animals become sedentary at the 3-setiger erpochaeta stage. Erpochaeta lack their ciliary crown and thus are completely benthic. The juvenile, benthic worm of 10 or 11 segments has the same style of life as adult. This kind of life cycle

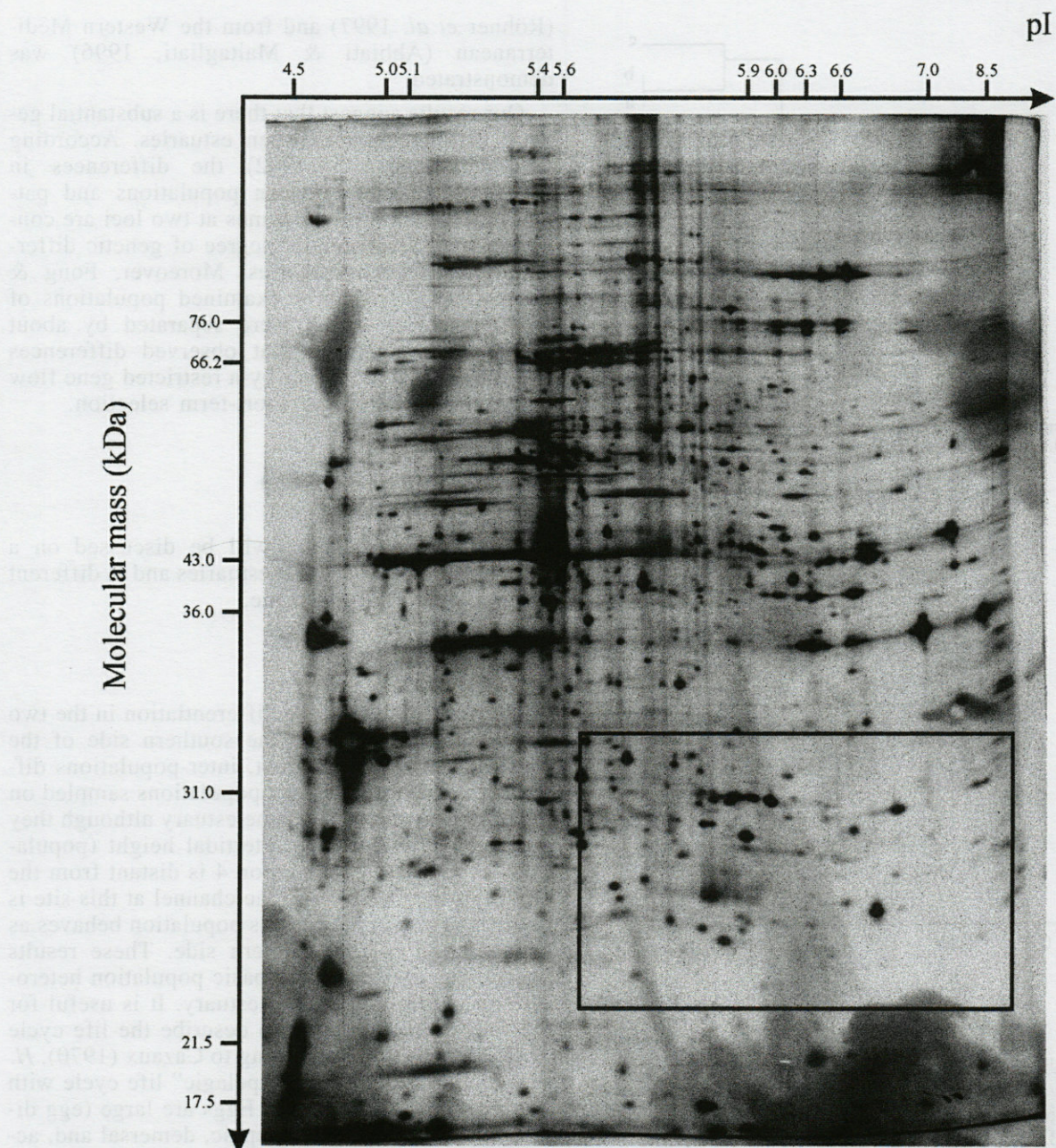


Fig. 6. – Example of an electrophoretic analysis of the water-soluble protein fraction in an extract of metameres of an individual of *Hediste diversicolor* collected in the Aa estuary. Proteins taken into account for the inter-individual comparisons are delineated by a rectangular area.

does not favour a great dissemination of larvae. As a consequence, protein similarity (general protein and non-specific esterase patterns) of the populations from the southern side of the Canche estuary could be explained by local marine currents which are more intense on the southern side of this estuary, favouring an orientated dissemination of larvae to the southern side and isolating populations from the opposite side.

Our results, showing an heterogeneity of populations within the Canche estuary are consistent with

those of Hateley *et al.* (1992) who found differences between populations within an estuary and interpreted them as indicating a limited amount of gene flow between sites located 1 km apart. However, patterns of variation at two loci provide only weak evidence for differentiation within estuaries and therefore did not allow these authors to provide an unequivocal conclusion. In other respects, in all breeding populations of *H. diversicolor*, the observed sex ratio is favorable to females. Herpin (1925) reported that the ratio of males to females

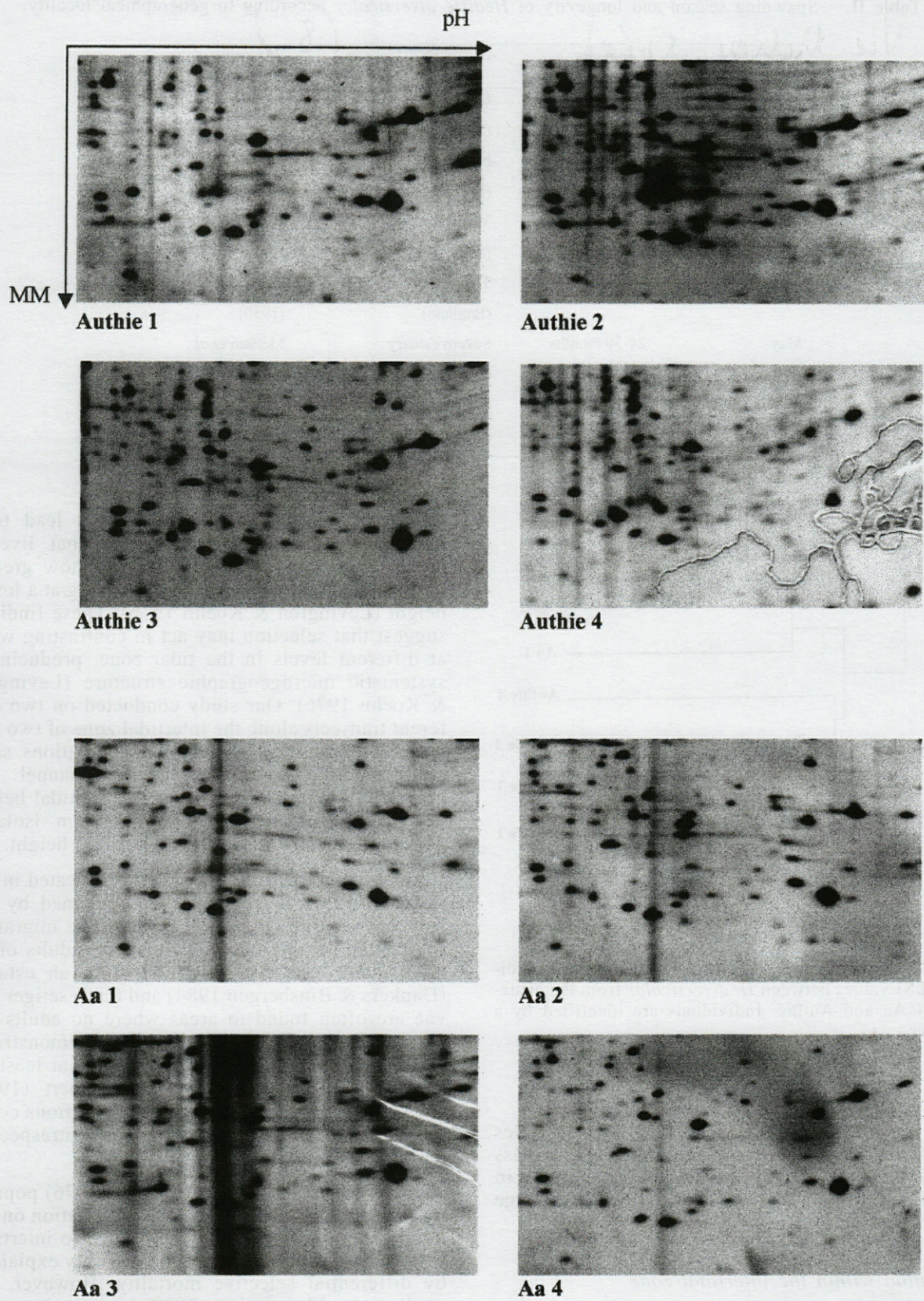
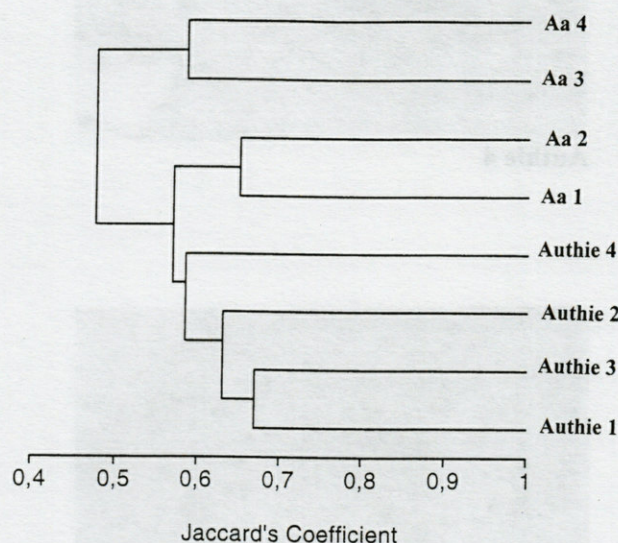


Fig. 7. — Detailed examples of inter-individual variations in the gels for the eight individuals studied.

Table II. – Spawning season and longevity of *Hediste diversicolor* according to geographical locality.

Spawning	Longevity	Geographical locality	Reference
May	24-36 months	Güteborg (Sweden)	Möller (1985)
February and April to August	12-18 months	Norsminde Fjord (Denmark)	Kristensen (1984)
January to March And June to August	18-24 months	Ythan estuary (Scotland)	Chambers and Milne (1975)
February	18 months	Thames estuary (England)	Dales (1950)
May	24-36 months	Severn estuary (England)	Mettam <i>et al.</i> , (1982)
March-April	36 months	Blyth estuary (England)	Olive and Garwood (1981)

Fig. 8. – UPGMA dendrograms derived from inter-individual SJ values between *H. diversicolor* from the estuaries of Aa and Authie. Individuals are identified by a number.

does not reach 1/7 at Cherbourg (France). Dales (1950) estimated the percentage of males to be less than 10% in the Thames estuary. This too argues in favour of very restricted gene flow and large founder effects.

Variation within the intertidal zone

The intertidal zone differs dramatically in exposure time, temperature, heat transfer, water retention (Newell 1979) and could provide an obvious

source of heterogeneity which could lead to a microgeographic variation. Species that live at higher levels in the intertidal zone show greater physiological tolerance than those living at a lower height (Levington & Koehn 1976). These findings suggest that selection may act in contrasting ways at different levels in the tidal zone, producing a systematic microgeographic structure (Levington & Koehn 1976). Our study conducted on two different transects along the intertidal zone of two different estuaries has shown that populations sampled along the same eroding channel are genetically identical whatever the intertidal height is, whereas populations sampled from isolated pools differ according to the intertidal height.

Genetic mixing of the populations located in the same eroding channel could be explained by the fact that eroding channels canalized the migration of "benthopelagic" larvae. However, adults of *H. diversicolor* can also migrate within an estuary (Dankers & Binsbergen 1984) and three-setiger larvae are often found in areas where no adults are present (Davey & Goerge 1986). This demonstrates the dispersal ability of *H. diversicolor* at least on small spatial-scales. Moreover, Lambert (1986) suggested that adults of Brittany populations could be displaced in channels when the intraspecific density is too high.

According to Levington & Koehn (1976) population genetics of mussels reveal that variation on the microgeographic scale may be related to intertidal height, mussel size and age, and possibly explained by differential selective mortality. However, according to Mustaquim (1988), successive year groups of *H. diversicolor* from the Blyth estuary (England) are not genetically different. Moreover, studies conducted on *Mytilus edulis* strongly sug-

gest that environmental factors are the main factor influencing allozyme variations (Levinton & Koehn 1976). According to this point of view, estuaries represent fluctuating environments and thus provide an obvious selective force towards spatial heterogeneity among populations. Moreover, some authors have shown the presence or the absence of some electrophoretic bands in relation to environmental conditions (d'Hondt & Goyffon 1986, Sin & Jones 1983). These authors explain these differences by selective mortality against heterozygotes. Kerambrun & Guérin (1984) noticed biochemical modifications in relation to stress and showed variations in zymograms in marine invertebrates in relation with dietary, pollution and thermic effects. Moreover, d'Hondt & Goyffon (1986) transferred populations from one site to another and showed that some enzyme systems could be inducible. Our results suggest that the inter-population variability of *H. diversicolor* within an estuary could be related to genetic (reduce gene flow) and ecophysiological (adaptation to fluctuant environments) factors. In the present state of our knowledge and in order to distinguish between these two processes, enzyme systems should be studied by reciprocal transplantation of individuals from one site to another to test their inducibility.

Inter-individual variation

Two-dimensional electrophoresis is a powerful tool to study protein variation between and among natural populations. According to Piñeiro *et al.* (1998) 2D-PAGE proves to be a valuable tool for the differential characterization among closely related *Meuluccius spp* (fish). 2D-PAGE was also used by Van der Beek *et al.* (1998) to study genetic variation among parthenogenetic plant-parasitic root-knot nematode species belonging to the genus *Meloidogyne*.

Surprisingly our results show a great inter-individual variability in protein profiles in 2D-PAGE. These results seem to corroborate the hypothesis of a restricted gene flow between populations of *H. diversicolor* rather than short term selection because in that case the inter-individual variability would be very low.

Two-dimensional electrophoresis allowed us to determine both the isoelectric points and molecular weights of the major water-soluble proteins and to perform protein characterization in the polychaete annelid *H. diversicolor*. Moreover, this data-base will now be used as a powerful tool to identify proteins in which synthesis is regulated in various experimental situations, in particular in toxicity test, since this species seems to be a good candidate for laboratory studies to test the toxicity of pollutants (Scaps *et al.* 1997).

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RÉPARTITION DES HÉTÉROPTÈRES AQUATIQUES (GERROMORPHA ET NEPOMORPHA) DE LA PROVINCE DE MADRID (ESPAGNE)

*Distribution of aquatic Heteroptera (Gerromorpha and Nepomorpha)
in the province of Madrid (Spain)*

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HÉTÉROPTÈRES AQUATIQUES
GERROMORPHA
NEPOMORPHA
DISTRIBUTION
MADRID
ESPAGNE

RÉSUMÉ. – La relation entre une série de variables environnementales quantitatives et qualitatives et la répartition des Hétéroptères aquatiques de la province de Madrid est étudiée en utilisant une technique d'analyse multivariée. La répartition des espèces du groupe Nepomorpha paraît être étroitement liée aux caractéristiques physico-chimiques de l'eau, alors que celle des espèces du groupe Gerromorpha dépend surtout du type de cours d'eau.

AQUATIC HETEROPTERA
GERROMORPHA
NEPOMORPHA
DISTRIBUTION
MADRID
SPAIN

ABSTRACT. – The relation between several environmental variables (qualitative and quantitative) and the distribution of aquatic Heteroptera of Madrid (Spain) is studied using a multivariate analysis. The distribution of Nepomorpha species was closely related to physical and chemical characteristics of water. However, Gerromorpha species were mainly related to water body type.

INTRODUCTION

Les Hétéroptères aquatiques pullulent dans pratiquement tous les types de milieux aquatiques épicontinentaux et constituent un groupe bien défini et relativement bien étudié, spécialement du point de vue taxonomique et faunistique ; au sujet de ce dernier aspect on peut citer des études qui prennent en compte l'ensemble de la Péninsule Ibérique (Nieser & Montes 1984, Baena & Vázquez 1986) ou une région ou une province déterminée (Fernandez Bernaldo de Quirós 1985, Lucas Castro 1988, López *et al.* 1995). Des aspects phénologiques et autoécologiques d'espèces déterminées ont également été étudiés (Sites & Nichols 1990, López *et al.* 1995, 1996, 1998). Cependant, il y a peu de données quantitatives concernant les facteurs environnementaux qui conditionnent la répartition des espèces de ce groupe.

La complexité des habitats aquatiques épicontinentaux d'une part, la relative indépendance de ces espèces vis-à-vis des conditions physico-chimiques de l'eau d'autre part – ce qui fait que les Hétéroptères aquatiques ne sont pas pris en considération

dans la détermination des indices biologiques de caractérisation de la qualité des eaux – et enfin, la grande mobilité et l'aptitude à la dispersion de la majorité de ces espèces leur permettant de pulluler dans tous les milieux, rendent de telles études difficiles à entreprendre.

Par ailleurs, la plupart des travaux publiés sur le sujet traitent quasi exclusivement des Corixidae (Macan 1938, 1954, Popham 1943, Savage & Pratt 1976, 1990, Murillo 1984, Tully *et al.* 1991).

Dans le présent travail, nous étudions la répartition de 45 espèces d'Hétéroptères aquatiques (31 Nepomorpha et 14 Gerromorpha) en fonction d'une série de variables de l'environnement. Nous sommes conscients, en accord avec Tully *et al.* (1991), du fait que ces variables peuvent ne pas agir directement sur la répartition des espèces considérées ; mais elles peuvent agir de manière indirecte, sur la disponibilité des ressources nutritives (Reynolds 1975), la présence de prédateurs (Macan 1965, Henrikson & Oscarson 1978, 1981, Eriksson *et al.* 1980) et sur l'existence de parasites intraspécifiques (Scudder 1983) ou encore sur n'importe quel autre facteur qui peut, à son tour, influencer cette répartition.

MATÉRIEL ET MÉTHODES

Durant 1988 et 1989, 26 stations de la province de Madrid, désignées chacune par une lettre alphabétique (Tabl. I), ont été échantillonnées. Chaque station a fait l'objet durant une année d'un échantillonnage semiquantitatif mensuel (García de Jalón & González del Tanago 1986), permettant de capturer le plus grand nombre possible d'espèces dans une zone déterminée. Une analyse comparative des données obtenues selon le temps d'échantillonnage a été réalisée en vue de déterminer la durée du prélèvement. Chaque opération d'échantillonnage a été menée en 2 périodes de 15 min séparées par un intervalle de temps durant lequel ont été mesurées les variables physico-chimiques des prélèvements d'eau.

Les captures ont été réalisées à l'aide d'un tamis circulaire de 18 cm de diamètre, 6 cm de concavité, 1 mm de maille et pourvu d'un manche d'aluminium de 1 m de longueur.

Parallèlement, une série de variables quantitatives (physico-chimiques) et qualitatives de l'environnement ont été mesurées.

Les variables quantitatives considérées sont l'altitude (m); la température de l'air et de l'eau (°C); l'oxygène dissout mesuré selon la méthode de Winkler, les résultats sont exprimés en pourcentage de saturation en oxygène après avoir été ajustés en fonction de la pression atmosphérique locale en utilisant les facteurs de correction tenant compte de l'altitude (Schwoerbel 1975); le pH, mesuré à l'aide d'un pH-mètre Crimson à 25 °C; la conductivité ($\mu\text{S} \cdot \text{cm}^{-2}$), mesurée à l'aide d'un conducti-

mètre Crimson à 25 °C; la teneur en chlorures mesurée suivant la méthode de valoration mercurimétrique en fonction du diphenylcarbazone, exprimée en mg/l; l'alcalinité totale ($\text{mg HCl} \cdot \text{l}^{-1}$), mesurée par la méthode de valoration acidimétrique en fonction d'un indicateur mixte (pH 4,3); la dureté totale ($\text{mmol} \cdot \text{l}^{-1}$), déterminée par la méthode de valoration complexométrique avec Triplex III en fonction d'un indicateur mixte. Afin d'uniformiser les résultats, toutes ces variables quantitatives ont été mesurées au laboratoire à 25 °C pendant les 24 h qui ont suivi la prise des échantillons, à l'exception de l'altitude, la température de l'eau et de l'air et la quantité d'oxygène dissout, mesurées dans chaque station au moment des prélèvements.

Les valeurs moyennes annuelles des variables mesurées à chaque station sont reportées dans le Tabl. I. Les catégories établies pour l'analyse statistique sont exprimées au Tabl. II.

Les variables qualitatives prises en considération sont : le type de milieu aquatique, l'environnement, et le substrat.

Une analyse de correspondances (CA) des données a été réalisée afin de représenter, dans un même graphique, les variables, les espèces et les stations d'échantillonnage et étudier la distribution des différentes espèces dans leurs stations respectives. L'analyse des correspondances permet une représentation simultanée des lignes et des colonnes d'une matrice de données; elle est surtout adéquate pour des matrices de type présence-absence, mais également pour le nombre d'exemplaires ou d'abondance des espèces (Levorel *et al.* 1991).

Tabl. I. – Valeurs moyennes annuelles des variables mesurées dans chaque station. AT : Altitude. TR : Température de l'air. TA : Température de l'eau. SO : Saturation en oxygène. AL : Alcalinité. CL : Chlorures. DT : Dureté totale. CA : Conductivité.

Annual average values of variables in each station. AT : Altitude. TR : Air temperature. TA : Water temperature. SO : Oxygen saturation. AL : Alkalinity. CL : Chlorates. DT : Total hardness. CA : Conductivity.

Stations	UTM	Variables quantitatives									Variables qualitatives		
		AT	TR	TA	SO	pH	AL	CL	DT	CA	Substrat	Environnement	Type de milieu aquatique
a- Río Guadalix	30TVL4215	825	16,9	13,0	77,4	7,3	2,7	32,7	1,6	417,7	Pierreux	Lotique	Rivière
b- Río Perales	30TVK0369	450	19,5	15,8	120,9	8,3	2,9	40,9	1,3	416,9	Aréneux	Lotique	Rivière
c- Río Manzanares	30TVK3583	575	17,1	13,1	78,2	7,2	1,1	28,3	0,6	216,3	Aréneux-Limoneux	Lotique	Rivière
d- Río Jarama-I	30TVL5631	700	18,6	14,7	90,2	7,5	2,4	13,2	2,6	496,7	Pierreux	Lotique	Rivière
e- Río Jarama-II	30TVK5192	650	20,7	15,2	61,3	7,6	3,4	25,5	2,2	547,8	Limoneux	Lotique	Rivière
f- Río Tajo	30TVK5132	480	16,7	15,3	97,5	8,0	3,8	128,3	6,5	1.499	Pierreux-Limoneux	Lotique	Rivière
g- Río Lozoya	30TVL3932	1.050	17,2	12,6	92,8	7,2	0,8	8,4	0,4	76,2	Pierreux-Aréneux	Lotique	Rivière
h- Río Tajuña	30TVK8464	650	18,2	13,2	87,4	8,0	4,9	23,2	4,6	841,2	Limoneux	Lotique	Rivière
i- Río Guadarrama	30TVK2069	500	15,3	12,8	46,4	7,2	2,8	50,2	1,4	518,3	Pierreux-Aréneux	Lotique	Rivière
j- Río de Las Puentes	30TVL1110	1.100	15,2	11,6	97,5	7,1	0,7	19,8	0,45	133,6	Pierreux	Lotique	Ruisseau
k- Arroyo Berruenco	30TVL5226	950	15,7	12,1	81,6	6,8	1,1	12,8	0,5	131,0	Pierreux-Aréneux	Lotique	Ruisseau
l- Arroyo Navahuerta	30TVL2703	900	18,1	13,4	96,8	7,0	0,6	9,9	0,2	71,4	Pierreux-Limoneux	Lotique	Ruisseau
m- Pantano de La Jarosa	30TVL0502	1.125	16,6	15,4	101,4	7,1	0,5	8,0	0,2	47,6	Limoneux	Lentique	Réservoir
n- Embalse de La Granjilla	30TVK0592	920	14,7	14,9	116,8	8,1	1,6	18,6	0,8	207,6	Rocheux-Aréneux	Lentique	Réservoir
ñ- Laguna del Parque de La Coruña	30TVK1398	900	16,6	14,2	51,8	7,4	3,5	67,0	4,8	991,2	Pierreux-Aréneux	Lentique	Lagune
o- Laguna de San Juan	30TVK5543	560	18,5	15,0	118,3	7,7	6,5	94,6	12,2	2.082	Limoneux-Argileux	Lentique	Lagune
p- Mar de Ontigola	30TVK4930	540	15,6	14,7	102,3	7,8	4,5	172,0	26,3	4.161	Limoneux	Lentique	Lagune
q- Laguna del Campillo	30TVK5864	550	20,5	17,6	90,6	8,1	3,1	129,7	4,8	1.418	Pierreux-Aréneux	Lentique	Lagune
r- Las Canteras	30TVL1301	925	17,8	15,5	98,4	7,6	1,5	16,3	0,8	218,5	Rocheux-Aréneux	Lentique	Mare permanente
s- Charca de las Navas del Rey	30TVK9471	650	19,6	16,6	93,4	8,3	3,0	140,0	3,0	848,0	Pierreux-Aréneux	Lentique	Mare permanente
t- Charcas de La Hoya de Pepe H.	30TVL2021	1.950	14,2	10,6	82,7	6,3	0,2	6,6	0,1	15,2	Limoneux	Lentique	Mares temporaires
u- Charcas del Refugio Zabala	30TVL2020	2.050	11,2	10,3	95,1	6,3	0,2	6,3	0,08	15,8	Limoneux	Lentique	Mares temporaires
v- Charcas de Los Santos de la H.	30TVK7884	900	14,5	11,5	90,9	7,9	2,1	15,6	1,3	261,0	Argileux	Lentique	Mares temporaires
w- Charcas del Puerto de Canencia	30TVL3524	1.524	9,4	9,2	78,3	6,3	0,6	15,8	0,2	67,4	Limoneux	Lentique	Mares temporaires
x- Charcas de Las Navas del Rey	30TVK9471	650	17,7	12,6	86,9	7,0	1,2	9,8	0,4	131,7	Limoneux	Lentique	Mares temporaires
y- Charca de los Molinos	30TVL0805	1.025	15,6	10,7	101,0	6,7	0,6	13,6	0,3	97,8	Limoneux	Lentique	Mares temporaires

Tabl. II : Catégories des variables considérées.
Classes considered in studied variables.

VARIABLES QUANTITATIVES	
VARIABLE	CATÉGORIES
Altitude	Alt1: 450 m - 983 m
	Alt2: 984 m - 1.517 m
	Alt3: 1.518 m - 2.051 m
Température de l'eau	TAg1: 9,2 °C - 13,4 °C
	TAg2: 13,5 °C - 17,7 °C
Température de l'air	TAi1: 9,4 °C - 15,0 °C
	TAi2: 15,1 °C - 20,7 °C
Saturation en oxygène de l'eau	Ox1: 46,4 % - 71,2 %
	Ox2: 71,3 % - 96,1 %
	Ox3: 96,2 % - 121 %
pH	pH1: 6,3 - 6,7
	pH2: 6,8 - 7,2
	pH3: 7,3 - 7,7
	pH4: 7,8 - 8,3
Alcalinité	Alc1: 0,2 mg / l - 2,3 mg / l
	Alc2: 2,4 mg / l - 4,5 mg / l
	Alc3: 4,6 mg / l - 6,7 mg / l
Chlorures	Cl1: 6,3 mg / l - 89,1 mg / l
	Cl2: 89,2 mg / l - 172 mg / l
Dureté totale	D1: 0,0 mmol / l - 8,7 mmol / l
	D2: 8,8 mmol / l - 17,4 mmol / l
	D3: 17,5 mmol / l - 26,3 mmol / l
Conductivité	C1: 15 µs / cm - 1.398 µs / cm
	C2: 1.398 µs / cm - 2.780 µs / cm
	C3: 2.781 µs / cm - 4.163 µs / cm
VARIABLES QUALITATIVES	
VARIABLE	CATÉGORIES
Type de milieu aquatique	Rio: Rivière
	Ary: Ruisseau
	Emb: Réservoir
	Lna: Lagune
	ChP: Mare permanente ChE: Mare temporaire
Environnement	Lot: Lotique
	Len: Lentique
Substrat	RA: Rocheux-Aréneux
	Pe: Pierreux
	PA: Pierreux-Aréneux
	Ar: Aréneux
	PL: Pierreux-Limoneux
	Li: Limoneux
	LA: Limoneux-Argileux Ac: Argileux AL: Aréneux-Limoneux

La matrice comprend les 26 stations échantillonnées et l'abondance de chacune des espèces capturées (Tabl. III) et les 12 variables (quantitatives et qualitatives) subdivisées en un ensemble de 42 catégories au total (Tabl. II). Pour pouvoir utiliser les variables quantitatives dans cette analyse, on a subdivisé chacune d'entre elles en intervalles de même longueur.

Nous avons également réalisé une analyse canonique des correspondances (CCA) pour réduire les axes du (CA) à des fonctions linéaires des variables environnementales et afin de déterminer quel pourcentage d'espèces des différentes stations est dû aux variables considérées.

Dans les deux types d'analyses, la variation dans la composition des espèces des stations a été mesurée par un facteur d'inertie égal à la somme des valeurs propres. En comparant le facteur d'inertie du CCA, I (CCA) à ce-

lui de CA, I (CA) on obtient un indice de corrélation MCR. $MCR = I (CCA) / I (CA)$, celui-ci étant égal au carré du coefficient de corrélation (Levorel *et al.* 1991). Toutes les analyses ont été réalisées à l'aide du software CANOCO (CANOnical Community Ordination; Agricultural Mathematics Group DLO BOX 100, 6.700 AC Wageningen. The Netherlands.)

Nous avons suivi Polhemus *et al.* (1995) pour déterminer les Nepomorpha et Andersen (1995) pour les Gerromorpha.

RÉSULTATS

5 696 individus adultes appartenant à 45 espèces incluses dans 10 familles ont été capturés (Tabl. III) :

NEPOMORPHA

Fam. Corixidae Leach, 1815

1. *Micronecta (Micronecta) minuscula* Poisson, 1929.
2. *Micronecta (Dichaetonecta) scholtzi* (Fieber, 1860).
3. *Cymatia rogenhoferi* (Fieber, 1864).
4. *Heliocoris vermiculata* (Puton, 1874).
5. *Corixa punctata* (Illiger, 1807).
6. *Corixa iberica* Jansson, 1981.
7. *Corixa panzeri* Fieber, 1848.
8. *Corixa affinis* Leach, 1817.
9. *Paracoris concinna concinna* (Fieber, 1848).
10. *Hesperocoris sahlbergi* (Fieber, 1848).
11. *Hesperocoris linnaei* (Fieber, 1848).
12. *Hesperocoris bertrandi* Poisson, 1957.
13. *Parasigara infuscata* (Rey, 1890).
14. *Sigara (Halicoris) stagnalis stagnalis* (Leach, 1817).
15. *Sigara (Vermicoris) lateralis* (Leach, 1817).
16. *Sigara (Vermicoris) scripta* (Rambur, 1840).
17. *Sigara (Pseudovermicoris) nigrolineata nigrolineata* (Fieber, 1848).
18. *Sigara (Sigara) janssoni* Lucas Castro, 1983.
19. *Sigara (Subsigara) scotti* (Douglas & Scott, 1868).
20. *Sigara (Retrocorixa) limitata limitata* (Fieber, 1848).

Fam. Pleidae Fieber, 1851

21. *Plea minutissima* Leach, 1817.

Fam. Notonectidae Latreille, 1802

22. *Notonecta glauca* Linnaeus, 1758.
23. *Notonecta obliqua* Thunberg, 1787.
24. *Notonecta viridis* Delcourt, 1909.
25. *Notonecta maculata* Fabricius, 1794.
26. *Anisops sardeus* Herrich
27. *Anisops marazanofi* Poisson, 1966.

Fam. Neucoridae Leach, 1815

28. *Ilyocoris cimicoides cimicoides* (Linnaeus, 1758).
29. *Naucoris maculatus maculatus* Fabricius, 1789.

Fam. Nepidae Popov, 1968

30. *Nepa cinerea* Linnaeus, 1758.
31. *Ranatra (Ranatra) linearis* (Linnaeus, 1758).

Tabl. III : Individus de chacune des espèces capturés et stations considérées.
Individuals of each species and stations studied.

S	STATIONS																			
	a	b	c	d	e	f	g	h	i	j	k	l	m	n	ñ	o	p	q	r	s
1				4																
2		20	64	70	78	29	13		15			6	53	78	49	131	90	50		51
3																3	5		2	1
4																	39			
5											1		1		2			17		1
6											1	15			1			10		7
7		3			1					1	2	3	12	84	17			6		8
8		32	1		10					2	2	3	2	27	4	1		1	47	1
9												3	1						1	
10	4						5			22	41	5	1					1	36	7
11			14									1			162	5	1		2	2
12											1								1	
13	9	1					4			74	40	68							18	6
14					1												1	1		
15	12	7		1	109				40		1		1	61		3	16		13	1
16		16			6												3			3
17	24	79					1		105	2	26	15			1				26	14
18			313		66		1		6				102	2	114	5			1	2
19												3	411		93				1	2
20	7	31			2						1	26	5	3				1	23	2
21		6			2				6	3		58	4		26	37	4		58	14
22	3									13	4			1	1			4	1	5
23	1										1		2						22	
24	1	3								4			2		2			2	3	1
25	3	7	2							17	31	10	3					49	4	5
26		49											1	67		8	3		28	5
27														2						66
28															1					
29	1	9		6						4		40	1		8	2	2		17	
30	2	1	2		1					9	5			1					2	
31										2		12		3						
32			2	26		1						2		27		19	5			
33	20	19	3	14	6		9	1	1	22	9	8		10			1		5	1
34											1									1
35		8		2	30						12	9								
36											1								6	
37																			12	
38										3		1								8
39		1		13			45			34									1	
40				14		54		5												
41			5	2																
42			4	1												1	1			
43	9	27	8	1	10		1	1	20	2	5	5	18	16				1	6	2
44	5	7					3		1	22	26	8	1	2				6	1	15
45	1	3		44	7		25					1		15	5	7		2		37

GERROMORPHA

Fam. Mesoveliidae Douglas & Scott, 1867

32. *Mesovelia vittigera* Horváth, 1895.

Fam. Hydrometridae Billberg, 1820

33. *Hydometra stagnorum* (Linnaeus, 1758).

Fam. Hebridae Amyot & Serville, 1843

34. *Hebrus (Hebrus) pusillus pusillus* (Fallén, 1807).

Fam. Veliidae Brullé, 1836

35. *Microvelia (Microvelia) pygmaea* (Dofour, 1833).

36. *Velia (Plesiovelia) caprai caprai* Tamanini, 1947.

37. *Velia (Plesiovelia) caprai bertrandi* Tamanini, 1957.

38. *Velia (Plesiovelia) saulii* Tamanini, 1947.

Fam. Gerridae Leach, 1815

39. *Aquarius najas* (De Geer, 1773).

40. *Aquarius cinereus* (Puton, 1869).

41. *Gerris (Gerriselloides) lateralis* Schummel, 1832.

42. *Gerris (Gerriselloides) asper* (Fieber, 1860).

43. *Gerris (Gerris) thoracicus* Schummel, 1832.

44. *Gerris (Gerris) gibbifer* Schummel, 1832.

45. *Gerris (Gerris) argentatus* Schummel, 1832.

Chaque espèce a été désignée par un numéro identifiant.

L'analyse des correspondances portant sur toutes les variables et les espèces avec le nombre d'espèces capturées montre que l'axe des ordonnées s'associe d'une part aux variables quantitatives qui mesurent la concentration des sels (dureté, chlorures, alcalinité, conductivité), au pH et aux tempéra-

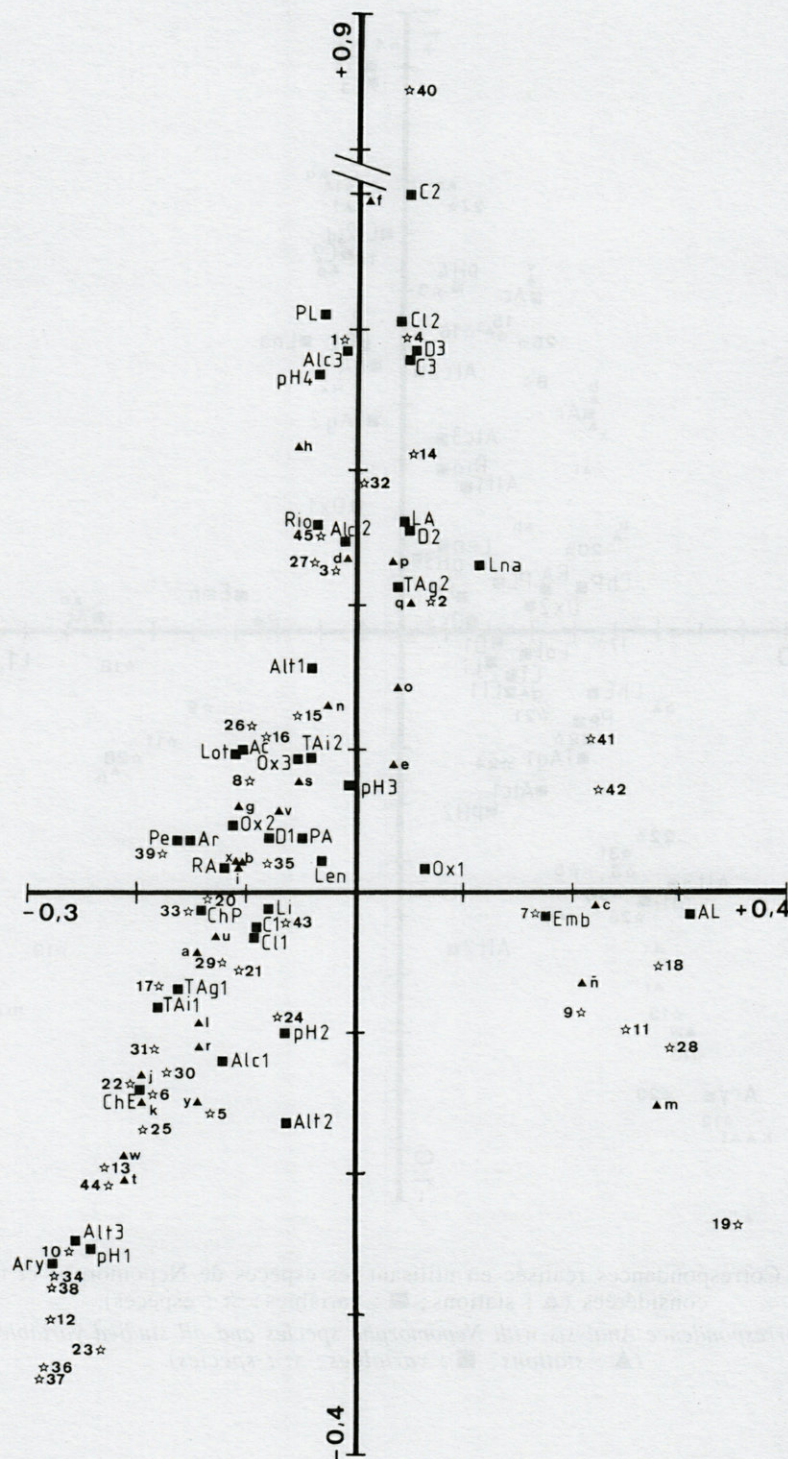


Fig. 1. Analyse des Correspondances réalisée en utilisant toutes les espèces et toutes les variables considérées (▲ : stations; ■ : variables; ☆ : espèces).

Correspondence Analysis with all studied species and variables (▲ : stations; ■ : variables; ☆ : species).

tures de l'air et de l'eau qui forment des gradients croissants allant des valeurs négatives vers les valeurs positives de l'axe. D'autre part il s'associe à l'altitude qui forme un gradient décroissant allant des valeurs positives vers les valeurs négatives.

Les espèces (Fig. 1) s'ordonnent d'une manière continue le long de cet axe. Ainsi (1) *Micronecta minuscula*, (4) *Heliocoris vermiculata* et (40) *Aquarius cinereus* se situent à l'extrémité du gradient correspondant aux zones de basses altitudes

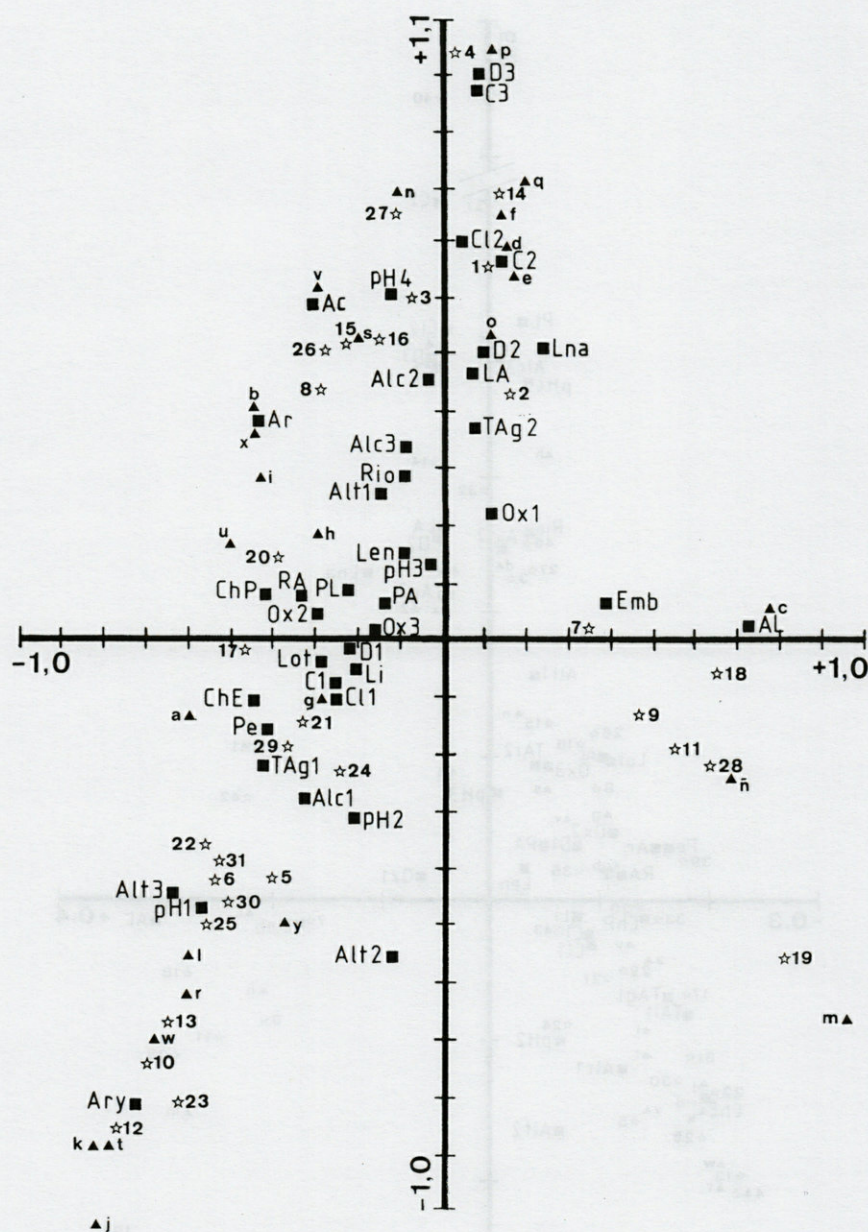


Fig. 2. Analyse des Correspondances réalisée en utilisant les espèces de Nepomorpha et toutes les variables considérées (▲ : stations; ■ : variables; ☆ : espèces).

Correspondence Analysis with Nepomorpha species and all studied variables
(▲ : stations; ■ : variables; ☆ : species).

et aux eaux tièdes basiques et de grandes concentrations en sels. A l'autre extrémité du gradient correspondant aux zones de hautes altitudes où les eaux sont froides, acides et quasi dépourvues de sels, on rencontre un groupe formé par (37) *Velia berlandi*, (36) *V. caprai caprai*, (23) *Notonecta obliqua*, (12) *Hesperocorixa berlandi*, (38) *V. saulii*, (34) *Hebrus pusillus*, (10) *H. sahlbergi* et (19) *Sigara scotti*. La majorité de ces espèces se répartissent d'une manière progressive entre les deux extrêmes indiquant ainsi qu'elles se répartissent

sur un large intervalle des variables considérées mais avec un léger déplacement vers les zones d'eaux de faible ou moyenne teneur en sels.

L'axe des abscisses est formé principalement par l'oxygène dissout et les variables qualitatives type de cours d'eau et type de substrat. En fonction de ces variables, l'ensemble formé par (41) *Gerris lateralis*, (42) *G. asper*, (7) *Corixa panzeri*, (18) *Sigara janssoni*, (9) *Paracorixa concinna*, (11) *Hesperocorixa linnaei*, (28) *Ilyocoris camicoides* et (19) *Sigara scotti* s'est séparé du reste.

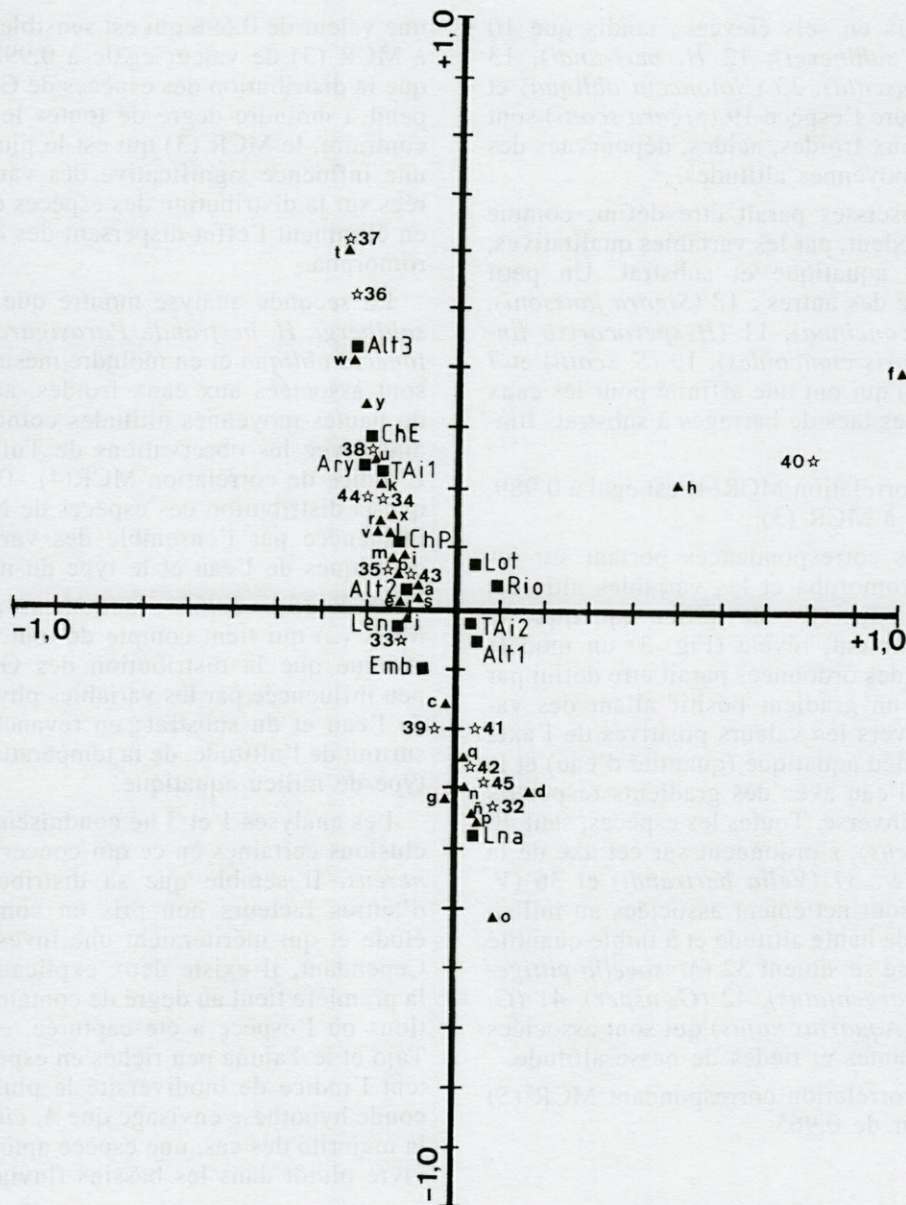


Fig. 3. Analyse des Correspondances réalisée en utilisant les espèces de Gerrromorpha et toutes les variables considérées (▲ : stations; ■ : variables; ☆ : espèces).

Correspondence Analysis with Gerromorpha species and all studied variables
(▲ : stations; ■ : variables; ☆ : species).

L'indice de corrélation global MCR (1) prend une valeur de 0,976.

Une seconde analyse des correspondances prend en compte, indépendamment les unes des autres, les espèces de Gerromorpha et celles de Nepomorpha, et seulement les variables qui ont, à priori, été considérées comme les plus influentes sur leur répartition. Les résultats obtenus sont les suivants :

L'analyse des correspondances des espèces de Nepomorpha avec toutes les variables, à l'exception de la température de l'air, révèle (Fig. 2) un

modèle similaire à celui de la Fig 1 : axe des ordonnées défini par les variables quantitatives (concentrations en sels, pH, température de l'eau) qui forment des gradients croissants allant des valeurs négatives vers les valeurs positives de l'axe et par l'altitude ayant un gradient croissant en sens opposé; les espèces se distribuent le long de cet axe d'une manière similaire à celle de la figure 1. Ainsi l'espèce 4 (*Heliocorisa vermiculata*) et, en moindre mesure, 1 (*Micronecta minuscula*), 27 (*Anisops marazanofi*) et 14 (*Sigara stagnalis*) sont associées aux basses altitudes d'eaux tièdes, basi-

ques et à teneurs en sels élevées; tandis que 10 (*Hesperocorixa sahlbergi*), 12 *H. bertrandi*), 13 (*Parasigara infuscata*), 23 (*Notonecta obliqua*) et en moindre mesure l'espèce 19 (*Sigara scotti*) sont associées aux eaux froides, acides, dépourvues des sels de hautes-moyennes altitudes.

L'axe des abscisses paraît être défini, comme dans le cas précédent, par les variables qualitatives, type de milieu aquatique et substrat. Un petit groupe se sépare des autres : 18 (*Sigara janssoni*), 9 (*Paracorixa concinna*), 11 (*Hesperocorixa linnaei*), 28 (*Ilyocoris cimicoides*), 19 (*S. scotti*) et 7 (*Corixa panzeri*) qui ont une affinité pour les eaux des lagunes et des lacs de barrages à substrats limno-sablonneux.

L'indice de corrélation MCR(4) est égal à 0,989, valeur similaire à MCR (3).

L'analyse des correspondances portant sur les espèces de Gerromorpha et les variables altitude, température de l'air, type de milieu aquatique et type d'environnement, révèle (Fig. 3) un modèle différent. L'axe des ordonnées paraît être défini par l'altitude, avec un gradient positif allant des valeurs négatives vers les valeurs positives de l'axe, et le type de milieu aquatique (quantité d'eau) et la température de l'eau avec des gradients respectifs positifs en sens inverse. Toutes les espèces, sauf 40 (*Aquarius cinereus*), s'ordonnent sur cet axe de la manière suivante : 37 (*Velia bertrandi*) et 36 (*V. caprai caprai*) sont nettement associées au milieu aquatique froid de haute altitude et à faible quantité d'eau. À l'opposé se situent 32 (*Mesovelina vittigera*), 45 (*Gerris argentatus*), 42 (*G. asper*), 41 (*G. lateralis*) et 39 (*Aquarius najas*) qui sont associées aux eaux abondantes et tièdes de basse altitude.

L'indice de corrélation correspondant MCR (5) prend une valeur de 0,965.

DISCUSSION

La première analyse des correspondances montre que l'ensemble des espèces *Gerris lateralis*, *G. asper*, *Corixa panzeri*, *Sigara janssoni*, *Paracorixa concinna*, *Hesperocorixa linnaei*, *Ilyocoris cimicoides* et *Sigara scotti* présente une affinité pour les milieux aquatiques faiblement oxygénés tels que les lagunes et les bassins de barrage à substrats limno-sablonneux.

L'indice de corrélation global MCR (1) indique que la variabilité observée dans la distribution de l'ensemble des espèces s'explique à 97,6 %, par l'influence des variables prises en considération. Si l'on compare cet indice à ceux calculés pour les espèces de Gerromorpha MCR (2) et de Nepomorpha MCR (3) en tenant compte des variables respectives considérées, on trouvera que MCR (2) prend

une valeur de 0,696 qui est sensiblement inférieure à MCR (3) de valeur égale à 0,998; ceci indique que la distribution des espèces de Gerromorpha dépend à moindre degré de toutes les variables. Au contraire, le MCR (3) qui est le plus élevé indique une influence significative des variables considérées sur la distribution des espèces de Nepomorpha en éliminant l'effet dispersant des espèces de Gerromorpha.

La seconde analyse montre que *Hesperocorixa sahlbergi*, *H. bertrandi*, *Parasigara infuscata*, *Notonecta obliqua* et en moindre mesure *Sigara scotti* sont associées aux eaux froides, acides, sans sels de hautes-moyennes altitudes coïncidant en partie ainsi avec les observations de Tully *et al.* (1991). L'indice de corrélation MCR(4) -0,989- confirme que la distribution des espèces de Nepomorpha est influencée par l'ensemble des variables physico-chimiques de l'eau et le type du milieu.

MCR (5) -0,965-, nettement plus élevé que MCR (2) qui tient compte de toutes les variables, indique que la distribution des Gerromorpha est peu influencée par les variables physico-chimiques de l'eau et du substrat; en revanche, elle dépend surtout de l'altitude, de la température de l'air et du type de milieu aquatique.

Les analyses 1 et 3 ne conduisent pas à des conclusions certaines en ce qui concerne *Aquarius cinereus*. Il semble que sa distribution obéisse à d'autres facteurs non pris en compte dans cette étude et qui mériteraient une investigation à part. Cependant, il existe deux explications possibles : la première tient au degré de contamination des stations où l'espèce a été capturée, en particulier le Tajo et le Tajuña peu riches en espèces qui présentent l'indice de biodiversité le plus faible. La seconde hypothèse envisage que *A. cinereus* est, dans la majorité des cas, une espèce aptère, elle pourrait vivre plutôt dans les bassins fluviaux.

CONCLUSION

La répartition des espèces de Nepomorpha capturée est influencée par l'ensemble des variables physico-chimiques de l'eau et par le type de milieu aquatique, le substrat et le type d'environnement lotique ou lentique. Quoique la majorité des espèces de ce groupe aient une grande capacité d'adaptation et une grande capacité à coloniser différents types de milieux aquatiques, il existe cependant un petit groupe d'espèces constitué par *Heliocoris vermiculata*, *Micronecta minuscula*, *Anisops marazanofi* et *Sigara stagnalis* qui pullulent dans les eaux tièdes, basiques et à fort contenu en sels minéraux. Un autre ensemble regroupe *Hesperocorixa sahlbergi*, *H. bertrandi*, *Parasigara infuscata* et *Notonecta obliqua* qui sont associées aux eaux

froides acides et presque dépourvues de sels minéraux.

La répartition des espèces de Gerromorpha paraît être influencée en moindre mesure par les variables physico-chimiques de l'eau et du substrat; elle dépend surtout de l'altitude et du type de milieu aquatique.

Seules *Velia caprai bertrandi* et *V. c. caprai* sont étroitement liées au milieu aquatique de haute altitude et par conséquent aux basses températures; cependant *Velia c. caprai* à large répartition dans la Péninsule Ibérique n'est pas exclusivement associée aux eaux froides.

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TAXINOMIE ET RÉPARTITION DES COPÉPODES PÉLAGIQUES PROFONDS DE MÉDITERRANÉE (AU LARGE DE MALTE)

Taxonomy and distribution of bathypelagic copepods from the Mediterranean Sea (off Malta)

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RÉSUMÉ. – Lors de la campagne Médiplanct, en 1972, des prélèvements de zooplancton ont été réalisés par des traits horizontaux en Méditerranée à différentes profondeurs, au large de Malte. L'analyse taxinomique des Copépodes pêchés entre 1 800 et 3 700 m a permis l'identification de 62 espèces. Contrairement à ce qui pourrait être attendu à de telles profondeurs, peu d'espèces typiquement bathypélagiques ont été identifiées. Elles semblent remplacées par des espèces à large distribution verticale. Cela constituerait la caractéristique de la faune méditerranéenne orientale de profondeur, et s'explique par les propriétés physico-chimiques de cette mer ainsi que par l'histoire de la formation des eaux méditerranéennes. Les pêches analysées se caractérisent aussi par la présence de trois espèces jusqu'alors non signalées en Méditerranée : *Aetideus acutus* Farran, 1929, *Spinocalanus terranovae* Damkaer, 1975, et *Euchaeta paraacuta* Tanaka, 1973.

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ABSTRACT. – The Mediplanct cruise, in 1972, permitted to realize samples of zooplankton using a technic of horizontal hauls, in the Mediterranean Sea off Malta. The taxonomic analysis of copepods between 1800 and 3700 meters led to the identification of 62 species. In contrast to results expected at such depth, few typically bathypelagic species were identified. They seem to be replaced by species with a large vertical distribution, which could explain the presence of more shallow living species. The faunistic composition may constitute the main characteristic of the eastern Mediterranean deep fauna, and can be explained by the physico-chemical properties of this sea as well as the historical formation of Mediterranean waters. These samples are also characterized by three species recorded for the first time in the Mediterranean Sea: *Aetideus acutus* Farran, 1929; *Spinocalanus terranovae* Damkaer, 1975; *Euchaeta paraacuta* Tanaka, 1973.

INTRODUCTION

Les premières pêches planctoniques profondes en Méditerranée datent du siècle dernier, mais n'ont été qu'épisodiquement reprises par la suite (Scotto di Carlo *et al.* 1984, 1991).

En Méditerranée orientale, la faune des eaux profondes n'est pas caractéristique de populations bathypélagiques à cause des éléments climatiques historiques qui caractérisent le bassin méditerranéen (Georges & Menzie 1968). Pour d'autres auteurs, la population des Copépodes de Méditerranée est cependant remarquable par l'absence de

dominance d'espèces typiquement bathypélagiques (Vinogradov 1968). Une des raisons avancée pour justifier cette distribution est la particularité des propriétés hydrologiques ou physico-chimiques du bassin (Sameoto 1986), bien différentes des conditions que l'on peut trouver dans un océan.

La campagne Médiplanct réalisée en 1972 a permis la récolte d'échantillons de grande profondeur par des traits horizontaux, et l'identification des Copépodes prélevés a conduit à une analyse taxinomique de 62 espèces, donnant un aperçu de la diversité des espèces vivant entre 1 800 et 3 700 m de profondeur.

Tabl. I. – Liste des espèces recensées, sexe observé et profondeur.
List of sampled species, observed sex, and depth.

<i>Calanoida</i>					
Familles	Espèces	Sexe	Profondeur (mètres)		
AETIDAEIDAE	<i>Aetideus acutus</i> Farran, 1929	F	2000	3000	
	<i>Aetideus giesbrechti</i> Cleve, 1904	F		3000	
	<i>Euchirella messinensis messinensis</i> (Claus, 1863)	F,M	2000	3000	
AUGAPTILIDAE	<i>Haloptilus longicornis</i> (Claus, 1863)	F	1500	2000	3000
	<i>Haloptilus plumosus</i> (Claus, 1863)	F		2000	
CALANIDAE	<i>Calanus helgolandicus</i> (Claus, 1863)	F		2000	
	<i>Nannocalanus minor</i> (Claus, 1863)	F	1500		
	<i>Neocalanus gracilis</i> (Dana, 1849)	F		2000	
CANDACIIDAE	<i>Candacia elongata</i> (Boeck, 1872)	F, juv	1500	2000	3000
	<i>Paracandacia bispinosa</i> (Claus, 1863)	F		2000	3000
CENTROPAGIDAE	<i>Centropages bradyi</i> Wheeler, 1901	F		2000	
CLAUSOCALANIDAE	<i>Clausocalanus parapergens</i> Frost et Fleminger, 1978	F		2000	
EUCALANIDAE	<i>Eucalanus hyalinus</i> (Claus, 1866)	F, juv		2000	3000
	<i>Pareucalanus << attenuatus >></i> (Dana, 1849)	F		2000	
	<i>Rhincalanus nasutus</i> Giesbrecht, 1888	F		2000	
	<i>Subeucalanus subtenuis</i> (Giesbrecht, 1888)	F		2000	
EUCHAETIDAE	<i>Euchaeta acuta</i> Giesbrecht, 1889	M		2000	3000
	<i>Euchaeta marina</i> (Prestandrea, 1833)	F			3000
	<i>Euchaeta paraacuta</i> Tanaka, 1973	F		2000	
HETERORHABDIDAE	<i>Heterorhabdus abyssalis</i> (Giesbrecht, 1889)	F		2000	3000
	<i>Heterorhabdus norvegicus</i> (Boeck, 1872)	M		2000	
	<i>Heterorhabdus papilliger</i> (Claus, 1863)	F		2000	
	<i>Heterorhabdus spinifrons</i> (Claus, 1863)	F		2000	
LUCICUTIIDAE	<i>Lucicutia clausi</i> (Giesbrecht, 1889)	F,M	1500	2000	3000
	<i>Lucicutia curta</i> Farran, 1905	F			3000
	<i>Lucicutia flavicornis</i> (Claus, 1863)	F,M	1500	2000	3000
	<i>Lucicutia gemina</i> Farran, 1926	F			3000
	<i>Lucicutia longiserrata</i> (Giesbrecht, 1889)	F	1500	2000	3000
	<i>Lucicutia pera</i> A. Scott, 1909	M			3000
MECYNOCERIDAE	<i>Mecynocera clausi</i> I.C. Thompson, 1888	F	1500	2000	
METRIDINIDAE	<i>Pleuromamma abdominalis abdominalis</i> (Lubbock, 1856)	F,M		2000	3000
	<i>Pleuromamma gracilis maxima</i> Steuer, 1931	F,M		2000	
PHAENNIDAE	<i>Onchocalanus trioniceps</i> Sars, 1905	F		2000	
PONTELLIDAE	<i>Pontella mediterranea</i> (Claus, 1863)	M		2000	
SCOLECITRICHIDAE	<i>Scolecithrix bradyi</i> Giesbrecht, 1888	F	1500		
SPINOCALANIDAE	<i>Monacilla typica</i> Sars, 1905	F		2000	
	<i>Spinocalanus magnus</i> Wolfenden, 1904	F		2000	
	<i>Spinocalanus spinosus</i> Farran, 1908	F		2000	
	<i>Spinocalanus terranova</i> Damkaer, 1975	F		2000	
TEMORIDAE	<i>Temora stylifera</i> (Dana, 1849)	M		2000	
<i>Mormonilloidea</i>					
MORMONILLIDAE	<i>Mormonilla minor</i> Giesbrecht, 1891	F		2000	
	<i>Mormonilla phasma</i> Giesbrecht, 1891	F			3000
<i>Cyclopoida</i>					
OITHONIDAE	<i>Oithona setigera</i> (Dana, 1849)	F	1500	2000	

Tabl. I. – (suite)
(continued)*Poecilostomatoidea*

CORYCAEIDAE	<i>Corycaeus (Agetus) flaccus</i> Giesbrecht, 1891	F,M	1500	2000	3000
	<i>Corycaeus (Agetus) limbatus</i> Brady, 1883	M			3000
	<i>Corycaeus (Agetus) typicus</i> (Kröyer, 1849)	F,M		2000	3000
	<i>Corycaeus (Corycaeus) clausi</i> F. Dahl, 1894	F,M		2000	
	<i>Corycaeus (Urocorycaeus) furcifer</i> Claus, 1863	F,M	1500	2000	3000
	<i>Farranula rostrata</i> (Claus, 1863)	F		2000	
ONCAEIDAE	<i>Lubbockia aculeata</i> Giesbrecht, 1891	F		2000	
	<i>Lubbockia squillimana</i> Claus, 1863	F			3000
	<i>Triconia conifera</i> Giesbrecht, 1891	M		2000	
	<i>Oncaea englishi</i> Heron, 1977	F		2000	
	<i>Oncaea mediterranea</i> (Claus, 1863)	F	1500	2000	3000
	<i>Oncaea ornata</i> Giesbrecht, 1891	F		2000	3000
SAPPHIRINIDAE	<i>Copilia vitrea</i> (Haeckel, 1864)	F			3000
	<i>Sapphirina intestinata</i> Giesbrecht, 1891	F			3000
	<i>Sapphirina metallina</i> Dana, 1849	F		2000	3000

Siphonostomatoidea

PONTOECIELLIDAE	<i>Pontoeciella abyssicola</i> (T. Scott, 1894)	F		2000	
RATANIDAE	<i>Ratania flava</i> Giesbrecht, 1892	F,M			3000

Harpacticoida

CLYTEMNESTRIDAE	<i>Clytemnestra rostrata</i> (Brady, 1883)	F			3000
	<i>Clytemnestra scutellata</i> Dana, 1848	F		2000	

MATÉRIEL ET MÉTHODES

Les échantillons analysés proviennent de la campagne Médiplanct (Bourdillon *et al.* 1974 ; Bhaud *et al.* 1974), effectuée en mer Ionienne du 15 au 20 juillet 1972, dans un secteur compris entre 35°15' et 35°45' de latitude nord, et 15°51' et 17°26' de longitude est. Les Copépodes analysés pour cette étude viennent des récoltes effectuées à l'aide de filets de type W.P.2 agrandi, ayant un diamètre d'ouverture de 1,5 m (soit une surface de 1,75 m²), une longueur totale de 7 m, et de vides de mailles de 200 µm. L'efficacité de filtration calculée est de 97 %. Parmi les échantillonnages réalisés, trois prélèvements simultanés ont été faits, à des profondeurs théoriques de 1 500 m, 2 000 m, 3 000 m. Ces échantillonnages ont duré 30 minutes, la vitesse de trait fixée à 0,5 m/s. Le volume ainsi filtré est de 1 500 m³. Les profondeurs réelles de prélèvements ont pu être évaluées indirectement, car les bathymètres utilisés avaient une limite d'utilisation à 1 500 m. Cette évaluation prend en compte la longueur de câble déroulée et la vitesse de trait. Aux prélèvements 1 500 m, 2 000 m, et 3 000 m correspondent respectivement les profondeurs réelles de 1 860 m, 2 480 m, 3 700 m.

L'étude hydrologique du secteur donne pour chaque profondeur la température, la salinité, et la teneur en oxygène :

— 23 FJ 1500 : T = 13,73 °C ; S = 38,705 ; [O₂] = 4,47 ml/L (77,1 % saturation),

— 23 FJ 2000 : T = 13,71 °C ; S = 38,684 ; [O₂] = 4,48 ml/L (77,4 % saturation),

— 23 FJ 3000 : T = 13,80 °C ; S = 38,660 ; [O₂] = 4,45 ml/L (76,9 % saturation).

Chaque échantillon de plancton a été fixé dès la fin du prélèvement, avec du formol neutralisé au borax, jusqu'à une concentration de 10 %.

L'identification des Copépodes commence par un tri préalable des femelles et des mâles, puis une reconnaissance morphologique par dissection des appendices. Les déterminations des genres et des espèces ont été faites à l'aide des ouvrages de Bradford 1972, Bradford-Grieve 1994, Heron & Bradford-Grieve 1995, Mauchline 1995, Mazzocchi *et al.* 1995, Markhaseva 1996 et Bradford-Grieve *et al.* 1999, et d'après la base de données sur les Copépodes planctoniques marins (C. Razouls & de Bovée in Observatoire Océanologique de Banyuls-sur-Mer : <http://www.obs-banyuls.fr>). Les observations s'effectuent à la loupe binoculaire et au microscope à contraste de phase.

RÉSULTATS

Dans les pêches 23 FJ 3000, 23 FJ 2000, et 23 FJ 1500, 62 espèces de Copépodes ont été identifiées, des femelles pour la plupart. La liste du tableau I indique les noms des espèces classées par famille,

le sexe des spécimens observés, et la profondeur de la pêche dont ils proviennent.

Concernant le sex-ratio des 62 Copépodes identifiés, 16,1 % ont un représentant de chaque sexe, 11,3 % sont strictement des mâles, et 72,6 % sont uniquement représentés par des femelles. Le sex-ratio observé s'explique par le biais introduit par l'échantillonnage et le tri des femelles en priorité.

DISCUSSION

Inventaire faunistique

On note la présence de 62 espèces, la Méditerranée et les mers annexes en totalisant 462 (Mazza 1966, Kovalev & Shmeleva 1982, Razouls 1995, 1996, Razouls & de Bovée sous presse). Ce nombre n'est pas surprenant d'après Scotto di Carlo *et al.* (1984, 1991), pour qui un aspect caractéristique de la Méditerranée profonde est son peuplement marqué par la présence de nombreuses espèces, et d'un faible nombre d'individus.

L'ouverture du canal de Suez en 1869 a entraîné la présence d'espèces indo-pacifiques en Méditerranée (Berdugo 1968, Casanova 1973, Lakkis 1976, 1984, 1990). Ces espèces, dites lessepsiennes, coexistent avec d'autres espèces d'origine endémique de la Méditerranée et des espèces immigrantes de l'Atlantique (Sewell 1948, Por 1969, Furnestin 1979) par le détroit de Gibraltar (Gaudy 1963, Seguin 1972, Greze *et al.* 1985). Dans ce cas et dans celui des espèces lessepsiennes, les espèces mésopélagiques et bathypélagiques ont à franchir un seuil de faible profondeur (320 m de profondeur seulement pour le détroit de Gibraltar) ce qui doit limiter leur pénétration.

Les espèces présentes uniquement dans l'Antarctique et la Méditerranée sont rares : *Oncaea pumilis* Heron, 1977 était la seule avant l'identification de *Spinocalanus terranova*. D'autres espèces ne sont présentes qu'en un nombre restreint de zones, comprenant la Méditerranée :

— zones sub-Antarctique, Indien : *Calocalanus longisetosus* Shmeleva, 1965.

— zones sub-Antarctique, Indien, et Canaries : *Calocalanus elongatus* Shmeleva, 1968, *C. gresei* Shmeleva, 1973.

— zones sub-Antarctique, Indien, Canaries, et Mer Rouge : *Calocalanus elegans* Shmeleva, 1965. D'autres espèces ont une répartition plus large :

— espèces originaires de l'Atlantique nord : *Calanus helgolandicus*, *Euchaeta marina*.

— espèces Indo-méditerranéenne : *Euchaeta pa-raacuta*, *Ratania flava*.

— espèce originaire de l'Atlantique : *Heterorhabdus norvegicus*.

— espèce méditerranéo-atlantique : *Pontella mediterranea*.

Les espèces restantes sont cosmopolites ou sporadiques dans les trois océans.

Répartition verticale

Généralement, le nombre d'espèces diminue avec la profondeur (Scotto di Carlo *et al.* 1991). Sur les trois pêches analysées en une seule station (23 FJ 1500, 23 FJ 2000, 23 FJ 3000), 62 espèces ont été identifiées, soit 13,4 % du total des espèces présentes en Méditerranée et des mers annexes. Cela représente une diversité assez importante, comparable à celle obtenue par Gaudy (1973) à partir de pêches réalisées à l'aide d'un bathyscaphe avec lequel il a recueilli 65 espèces sur 8 stations profondes au large des Açores.

La répartition verticale des espèces identifiées ici est dans certains cas surprenante. En effet, certaines espèces sont des formes eurybathiques interzonales ou subsuperficielles, et se retrouvent alors à des profondeurs inhabituelles. Il ne ressort aucune dominance d'espèces typiquement bathypélagiques, contrairement à ce que l'on aurait pu attendre.

Parmi les espèces se trouvant à une profondeur inhabituelle, certaines sont connues pour être strictement épipélagiques. Il s'agit de *Aetideus acutus*, *Haloptilus longicornis*, *Mecynocera clausi*, *Subeucalanus subtenuis*, *Temora stylifera*, *Farranula rostrata*.

Les espèces caractéristiques des profondeurs sont : *Candacia elongata*, *Eucalanus hyalinus*, *Euchaeta marina*, *Lucicutia longiserrata*, *Lucicutia pera*, *Monacilla typica*, *Ratania flava*.

D'autre part, la famille des Scolecitrichidae n'est ici représentée que par une seule espèce : *Scolecithrix bradyi*. Ceci est étonnant car cette famille comprend 42 espèces en Méditerranée, occidentale pour la plupart, qui sont généralement bathypélagiques (Scotto di Carlo *et al.* 1984).

Les espèces restantes sont épipélagiques à bathypélagiques ou épipélagiques à mésopélagiques.

Ceci peut s'expliquer par les caractéristiques physico-chimiques de la Méditerranée, alors que les références concernant la répartition verticale se situent pour la plupart dans les océans Atlantique et Indien.

La structure hydrologique verticale de la Méditerranée est peu comparable à celle d'un océan : à des profondeurs équivalentes, la température et la salinité y sont très différentes.

Une autre théorie avancée pour expliquer la présence d'espèces des niveaux supérieurs en zone ba-

thyale est celle des migrations d'espèces selon des cycles annuels ontogéniques, certaines espèces comme *Calanus helgolandicus* sont en profondeur pendant la saison chaude (Gaudy 1972).

Si les facteurs physico-chimiques des océans constituent une barrière à la présence des espèces de surface au niveau bathypélagique, ce n'est pas le cas en Méditerranée orientale où les eaux profondes conservent une température supérieure à 13 °C et une salinité supérieure à 38 ‰. Une espèce du niveau épipélagique ou mésopélagique n'aura donc aucun effort d'adaptation à faire en descendant au niveau bathyal. Le seul facteur pouvant encore influencer la répartition verticale est la lumière nécessaire à la production primaire. Les Copépodes filtreurs ne trouvent donc pas dans ces couches le phytoplancton dont ils se nourrissent habituellement vers la surface. C'est pourquoi, selon Vinogradov (1968), 60 à 80 % du plancton vivant entre 1 500 et 3 000 m est constitué de formes carnivores. Sous le niveau 3 000-4 000 m, le comportement carnivore est moins justifié du point de vue énergétique (du fait de la raréfaction des proies), les euryphages vont y prendre place et dominer dans les couches inférieures. L'étude en cours des mandibules devrait permettre une approche du régime alimentaire des Copépodes identifiés.

L'absence d'une faune bathypélagique caractéristique s'explique par des événements climatiques historiques dans la formation des eaux profondes du bassin méditerranéen. George & Menzie (1968) estiment qu'elles se différencient depuis environ 7 000 ans, date de l'isolement du bassin. Ce temps ne serait pas suffisant pour permettre l'apparition de populations spécifiques de profondeur et la réintroduction d'espèces profondes d'origine atlantique ou en provenance de la mer Thyrrénienne du fait du seuil siculo-tunisien.

Comparaison avec d'autres auteurs

Beaucoup des espèces identifiées ici sont les mêmes que celles signalées dans d'autres campagnes. Il n'est pas possible de faire une analyse de toutes les listes de Copépodes établies en Méditerranée, mais il est intéressant de comparer ces données avec celles fournies par quelques auteurs ayant analysé des pêches profondes, comme par exemple Vinogradov (1968). Dans la zone nord Atlantique, il note la dominance en profondeur des Euchaetidae, Lucicutiidae, et des Heterorhabdidae. Le maximum d'abondance des Euchaetidae, soit 61 % de cette population, se situe entre 2 000 et 4 000 m, tandis que 59 % des Lucicutiidae se trouvent aussi à ce niveau, alors que pour les Heterorhabdidae, 56 % de leur effectif se trouve à des profondeurs inférieures à 6 000 m. Pour la Méditerranée, il dresse une liste des Copépodes vivant à

plus de 1 000 m. Parmi les espèces rencontrées aussi dans nos prélèvements, *Calanus helgolandicus**, *Neocalanus gracilis**, *Euaetideus giesbrechti*, *Spinocalanus magnus*, *Euchaeta acuta*, *Euchirella messinensis*, *Lucicutia longiserrata*, *Heterorhabdus papilliger*, *Candacia bispinosa**, *Pleuromamma abdominalis*, *Copilia vitrea**, aucune n'est strictement inféodée à la zone profonde, mais elles ne s'observent généralement pas dans les niveaux supérieurs. Les espèces marquées d'un astérisque ne descendent généralement pas à plus de 1 000 m dans l'océan, mais peuvent dépasser 2 000 m en Méditerranée (comme le démontre nos résultats). A ces mêmes niveaux, Grice & Hülsemann (1967) signalent les familles suivantes : Scolecitrichidae, Lucicutiidae, Augaptilidae, Bathypontiidae dans les eaux tropicales, et les familles des Calanidae, Metridinidae, Aetideidae, Lucicutiidae, Euchaetidae, Augaptilidae dans le nord Pacifique. Dans cette zone, mais à des profondeurs plus importantes (entre 6000 et 8000 m), ils signalent trois familles principales : Scolecitrichidae, Metridinidae, Spinocalanidae. En 1984, Scotto di Carlo *et al.* font paraître le résultat d'une campagne en Mer Tyrrhénienne (Méditerranée) avec des prélèvements allant de la surface à 3 000 m. Ils y citent au total 140 espèces en dessous de 1 000 m, seulement 50 restent présentes. Elles sont 39 à 1 500 m, et elles ne sont plus que 25 sous 2000 m. Trois espèces font leur apparition à partir de 1 000 m : *Lucicutia longiserrata*, *Undinella stirni*, *Onchocalanus trigoniceps*. Parmi les 39 espèces situées à plus de 1 500 m, 22 ont été retrouvées dans nos prélèvements.

Böttger-Schnack (1990, 1997) a étudié la répartition des Copépodes Cyclopoïdes en Mer Rouge et en Méditerranée orientale, aux niveaux épipélagique et mésopélagique supérieur. La présence d'espèces communes dans ces 2 niveaux ne fait qu'accentuer le caractère non typiquement bathypélagique des Copépodes pélagiques de la Mer Rouge (Böttger-Schnack 1999) comme pour les profondeurs de la Méditerranée orientale.

Weikert & Koppelman (1993) établissent une comparaison de la répartition verticale des Copépodes entre l'Atlantique nord-est, la Mer Levantine, et la Mer Rouge. Les familles dominantes en profondeur sont, pour l'Atlantique les Heterorhabdidae, en Mer Levantine, les Eucalanidae, et au-dessous de 2 050 m les Lucicutiidae (notamment *L. longiserrata*, puis *L. pera* et *L. curta*). Il en est de même au sud-est de la Crête (Weikert & Trinka 1990). En Mer Rouge, à partir de 900 m, les familles qui dominent sont les Scolecitrichidae et les Lucicutiidae.

Il est possible de déduire de ces travaux une certaine continuité dans la diversité des espèces, comme le fait remarquer Scotto di Carlo (1991). On note dans les échantillons Médiplanct un manque d'espèces typiquement bathypélagiques, mais la faune présente (nombreux Lucicutiidae,

Augaptilidae, Metridinidae) semble spécifique de la Méditerranée profonde.

CONCLUSION

Les Copépodes analysés dans les pêches faites en profondeur au cours de cette campagne peuvent surprendre par leur caractère plus épi-mésopélagique que bathypélagique. Seulement sept espèces sur les 62 identifiées sont caractéristiques des profondeurs, ce qui est peu pour des pêches atteignant plus de 3 000 m. Les autres Copépodes constituent pourtant une faune de profondeur spécifique à la Méditerranée. La présence dans nos échantillons d'espèces appartenant aux Lucicutiidae, Heterorhabdidae, Eucalanidae, Metridinidae aux niveaux bathypélagiques corroborent les résultats obtenus lors de campagnes précédentes en Méditerranée.

Vinogradov (1968) proposait une séparation entre les formes de surface et profondes, en suggérant que les Copépodes mésopélagiques ne pouvaient pas prendre la place de formes limitées à la profondeur. Les zonations concernant une coupe verticale effectuée par Scotto di Carlo *et al.* (1984) en Mer Tyrrhénienne les conduisent à contester cette théorie : pour eux, la communauté profonde méditerranéenne présente un caractère original car elle est essentiellement constituée d'espèces de zone intermédiaire ayant une ample distribution verticale. Ce phénomène semble plus accentué en Méditerranée orientale du fait du seuil siculo-tunisien pour des raisons climatiques historiques (George & Menzie 1968) et ses propriétés physico-chimiques (Vinogradov 1968, Weikert & Koppelman 1993).

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MACROFAUNA ASSOCIATED WITH *PHYLLOCHAETOPTERUS SOCIALIS* AGGREGATIONS IN THE SOUTHWESTERN ATLANTIC

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POLYCHAETES
REFUGES
MACROFAUNA
BIOGENIC STRUCTURES
RÍO DE LA PLATA ESTUARY

ABSTRACT. – Aggregates of *Phyllochaetopterus socialis* Claparède, 1868 have been found near the Río de la Plata mouth (35° 23' – 35° 31' S; 55° 36' W – 55° 48' W) in November 1997. The depth of the sandy bottom was 11-12 m and the water salinity was 26-30‰. Each aggregate (ca. 20 cm diameter) arose from a shell or another small hard object. The macrofauna associated with these aggregates was studied and the results were compared with the available information on hard and soft bottom benthic communities in this area. The more abundant taxa registered were Polychaeta, Mollusca, Bryozoa and Decapod Crustacea. Several sessile species (serpulid polychaetes, thoracic cirripedia, bivalves, bryozoa and ascidiae) grow on the tubes. On the other hand, various polychaete and bivalve species, Anomura and Brachyura Decapod crustaceans and Ophiuroidea find refuge in the spaces between tubes. The macrofauna associated with the aggregates is more diverse than those found in the neighbourhood. The polychaete species belong to different trophic guilds; several species were recorded for the first time in the region and the distribution range of other species was extended. The importance of *P. socialis* aggregates in structuring marine benthic communities is discussed.

POLYCHÊTES
REFUGES
MACROFAUNE
STRUCTURES BIOGÉNIQUES
ESTUAIRE DE RÍO DE LA PLATA

RÉSUMÉ. – Des amas de tubes formés par l'Annélide Polychète *Phyllochaetopterus socialis* Claparède, 1868 ont été découverts et étudiés dans l'estuaire du Río de la Plata (35° 23' – 35° 31' S; 55° 36' W – 55° 48' W) en novembre 1997. La profondeur du fond sableux est de 11-12 m et la salinité de l'eau 26-30 ‰. Chaque amas (20 cm de diamètre en moyenne) a pour base une coquille ou un autre objet dur de faible dimension. L'inventaire de la macrofaune associée à ces amas est réalisé et les résultats sont comparés aux informations disponibles concernant les communautés benthiques de fonds durs et de fonds meubles de la région. Les taxa les plus abondants numériquement appartiennent aux Polychètes, Mollusques, Bryozoaires et Crustacés Décapodes. Plusieurs espèces sessiles (Polychètes Serpulidae, Cirripèdes thoraciques, Bivalves, Bryozoaires et Ascidies) se développent sur les tubes. En outre, des espèces variées de Polychètes, de Bivalves, de Crustacés Décapodes Anomoures et Brachyours, et d'Ophiurides sont récoltées entre les tubes. La macrofaune associée aux amas est plus diverse que celle récoltée dans le voisinage. Les Annélides Polychètes appartiennent à différents groupes trophiques. Plusieurs espèces sont signalées pour la première fois dans la région et la répartition d'autres espèces est élargie. L'action de structuration des communautés benthiques par les amas de tubes de *P. socialis* est discutée par les auteurs.

INTRODUCTION

Some marine benthic organisms create biogenic structures which provide structural complexity due to their intricate architectural forms: seagrasses, seaweed, sponges, hydrozoa, corals, polychaetes, molluscs and bryozoans (Nalesso *et al.* 1995 for a review). These structures are then colonized by other species that obtain food and shelter from predators or physical disturbances. Among polychaetes,

many Serpulidae build large biogenic structures, often called "heads" or "reefs", (e.g. *Filograna implexa*, *Serpula vermicularis* and *Ficopomatus enigmaticus*, among others) (Bianchi & Morri 1994), and some Sabellariidae (the European *Sabellaria alveolata* and its new-world counterpart *Phragmatopoma lapidosa*) form extensive "reefs" or bioherms in shallow waters (Pinheiro *et al.* 1997, Wilson 1976). On the other hand, the Onuphidae *Diopatra cuprea* (Woodin 1978) and the Chaetopteridae *Phyllochaetopterus socialis* (Gettleson

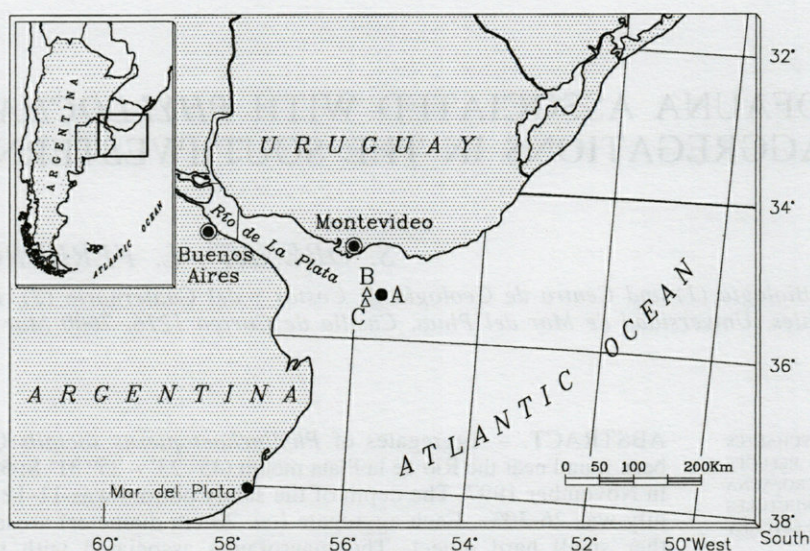


Fig. 1. – Location map and sampling sites (A, B, C). The analysed sample is denoted with a black circle.

et al. 1985, Nalesso *et al.* 1995) could be considered “refuge-forming” species. All these worms construct tubes, which are calcareous (Serpulidae), made of sand particles and a mucoproteinaceous cement (Sabellariidae, Onuphidae) or only organic (Chaetopteridae); the tubes may eventually coalesce to form large colonies.

The family Chaetopteridae always presents palps of varying lengths. Anterior region has uniramous parapodia; median and posterior regions have biramous parapodia. Setae include capillary, limabate setae and modified spines in setiger 4. The genus *Phyllochaetopterus* has a pair of small tentacular cirri at the base of the large palps. Median notopodia are foliaceous, bilobed and asetigerous. Neuropodia of the median and posterior region have pectinate uncini (Fauchald 1977). *Phyllochaetopterus socialis* Claparède, 1868 is a “small worm seldom exceeding 30 mm length and dark green posteriorly” (Day 1967) which lives in horny tubes, ringed distally, with ramifications, “often aggregated into branching colonies”. It is worldwide distributed in coastal waters, from 10 to more than 300 m, and is found on different substrates (muddy, sandy or rocky bottoms) (Abbiati *et al.* 1994). The cosmopolitanism of this species is not accepted by all authors (M. Bhaud, pers comm) and the specific name is probably wrong; however face to the absence of pertinent arguments we retain the traditional identification.

There are reports of the presence of *P. socialis* in the Atlantic Ocean, from the USA and the English Channel south to the Falkland (Malvinas) Islands and South Africa, the Mediterranean Sea, the Indian and Pacific Oceans and Australia. Abbiati *et al.* (1994) review the geographic distribution of this species; there are new records from Brazil

(Nalesso *et al.* 1995), Rio de la Plata (this paper) and the Argentine continental shelf, 14-30 miles away Mar del Plata (R. Elías, pers comm). Macrofaunal assemblages associated with colonies of *P. socialis* have been described from intertidal (Nalesso *et al.* 1995), 14 m depth (Felder & Chaney 1979) and 50/60 m depth (Gettleson *et al.* 1985) populations.

The aim of this paper is to characterize the macrofauna associated with *Phyllochaetopterus socialis* aggregations in an estuarine subtidal habitat in the southwestern Atlantic and to compare it with other epibiotic communities inhabiting this and other polychaete species.

MATERIAL AND METHODS

Aggregates of *Phyllochaetopterus socialis* have been collected on November 20, 1997, in the mouth of the Rio de la Plata (Fig. 1), by fishing trawls during the BIN Dr Eduardo Holmberg cruise H12/97. The hydrographic conditions are summarized in Table I. On arriving on board, the aggregates were fixed with 4% formaldehyde solution. In the laboratory, 12 aggregates were carefully broken, large organisms were removed by hand, and the remaining debris were washed with tap water through a sieve (0.35 mm mesh). The total sample volume was measured by water displacement. The organisms registered in the aggregates were classified and their relative abundance were estimated as follows: rare (1 individual), scarce (2-5 individuals), abundant (5-20 individuals), and very abundant (> 20 individuals). Poriferans, bryozoans and some polychaetes were identified by E Cuartas, JJ López Gappa and R Elías, respectively. All the polychaete specimens present in the two best preserved aggregates were counted and the species assigned to a feeding guild classification (Fauchald & Jumars 1979)

Table I. – *Phyllochaetopterus socialis*.
Sampling sites of the aggregates and their hydrographic conditions.

sampling site	latitude	longitude	depth (m)	temperature (°C)	salinity (‰)	bottom
A	35°23'S	55°36'W	12	17.3	29.9	sandy
B	35°23'S	55°48'W	11.5	17.8	26.7	sandy
C	35°31'S	55°48'W	11	17.4	28.8	sandy

according to their nutrition type, motility and pharyngeal structures.

RESULTS

Mats were attached to rocky substrates or empty mollusk shells, and supported a diverse fauna. Eleven phyla were represented: Porifera, Cnidaria, Nemertea, Nematoda, Annelida, Sipuncula, Mollusca, Arthropoda (Crustacea), Bryozoa, Echinodermata and Chordata (Urochordata) (Table II). The available information on the habitat of most of the specimens identified at the species level (in other localities) is summarized in Table III.

The sessile fauna include Demospongiae (Porifera) attached to the tubes and incrusting the hard basis, scarce colonies of *Sertularella striata* (Cnidaria: Hydrozoa), abundant individuals of an indetermined sea anemone, and five bryozoan genera that covers the tubes (although *Aetea anguina* and *Electra monostachys* are also registered on the basis). Abundant *Balanus improvisus* (Cirripedia: Thoracica) and *Corella* sp. (Ascidiacea) are observed on the tubes.

Between the tubes and on the basis there are abundant nemertean, nematoda and polychaete worms. The Sipuncula *Themiste petricola* is found on the hard substrate and densely intertwines among the tubes. Few specimens of *Ophiotrix angulata* and another indetermined ophiurid living between the tubes are the only echinoderms collected.

The total number of polychaetes in the two best preserved *Phyllochaetopterus socialis* mats (250 and 550 ml respectively) is 1682. The percentage of polychaete families found in these mats is shown in Table IV. The most abundant polychaetes belong to the Serpulidae (78%) and the Terebellidae (10%) in mat #1, Syllidae (58%) and Cirratulidae (11%) in mat #2. Most species belong to the filter-feeder/sessile/tentaculate guild (#1) and to the carnivore/motile/jawed guild (#2). Both mats presented surface deposit-feeder/sessile/tentaculate polychaetes and a low percentage of subsurface deposit-feeder/carnivore/motile/jawed (or with eversible sac-like pharynx) polychaetes. Herbivorous polychaetes are absent.

The most abundant molluscs are the bivalves *Lithophaga patagonica*, *Mytilus edulis platensis* and *Hiatella solida*. The bivalves *Musculus viator*, *Lyonsia patagonica*, *Sphenia hatcheri* and *Crassinella marplatensis* are less represented. The bivalves *Gastrochaena carcellessi*, *Brachydontes* sp., *Crassinella lunulata* and the gastropod *Caecum antillarum* are seldom registered. Among the bivalves, *Lithophaga patagonica* is found boring in the hard substrate which forms the basis of the mat and the other species are found attached to the tubes or living in the soft sediment trapped among them.

The decapod crustacean fauna associated with *P. socialis* aggregates consists of two porcellanids crabs (*Pachycheles haigae* and *P. chubutensis*) and one xanthid crab (*Pilumnus reticulatus*) that find shelter between the tubes.

DISCUSSION

The Rio de la Plata is a large, funnel-shaped, estuary which drains the vast Paraná-Uruguay hydrographic basin, the largest in South America after the Amazon River (Urien 1972). It is 270 km long and its width varies from 32 to 230 km. The sediment distribution represents a textural gradation from sands and silty sands, silts and clayed silts, with dispersal rocks and mollusc valves (Urien 1966, Urien *et al.* 1996). Thus, because of the sedimentological characteristics, the bottom of Rio de la Plata represents a monotonous environment and the *Phyllochaetopterus socialis* mats may be a source of variation in the structure of substratum.

The Polychaeta, Mollusca, Bryozoa and Decapod crustacean fauna of *Phyllochaetopterus socialis* aggregates is more diverse than the fauna found in the surrounding benthic communities. Roux & Bremec (1996) studied the benthic communities of the estuary along a transect from the shallow and brackish waters of the Rio de la Plata to the adjacent continental shelf and found 4, 9, 0, 1 species of Polychaeta, Mollusca, Bryozoa and Decapod crustacean respectively. In the mats of *P. socialis*, we found 28 species of polychaetes, 10 of

Table II. – *Phyllochaetopterus socialis*. Macrofauna associated with 12 aggregates and their microhabitats. R: rare, S: scarce, A: abundant, V: very abundant (1, 2-5, 5-20 and > 20 individuals respectively, * more than 400 individuals).

	epizoic, living on the tubes	sheltered, living between the tubes	epifaunal, living on the "basis"	infaunal, living buried in the "basis"	abundance
Phylum Porifera					
Class Demospongiae					
Order Hadromerida					
genus et species indeterminate	x				A
Order Axinellida					
<i>Suberites</i>	x		x		S
genus et species indeterminate	x		x		S
Phylum Cnidaria					
Class Hydrozoa					
<i>Sertularella striata</i>	x				S
genus et species indeterminate	x				R
Class Anthozoa					
Subclass Hexacorallia	x				V
Phylum Nematoda		x	x		V
Phylum Nemertea		x			S
Phylum Sipuncula					
<i>Themiste petricola</i>				x	V
Phylum Arthropoda					
Subphylum Crustacea					
Order Cirripedia					
<i>Balanus improvisus</i>	x				V
Order Decapoda					
<i>Pachycheles haigae</i>		x			S
<i>Pachycheles chubutensis</i>		x			S
<i>Pilumnus reticulatus</i>		x			S
Suborder Amphipoda		x			A
Subclass Ostracoda		x			A
Phylum Mollusca					
Class Bivalvia					
F. Anomiidae					
<i>Pododesmus sp</i>	x				S
F. Mytilidae					
<i>Mytilus edulis platensis</i>	x				A
<i>Musculus viator</i>	x				A
<i>Lithophaga patagonica</i>				x	A
<i>Brachydontes sp.</i>	x				S
F. Lyonsidae					
<i>Lyonsia patagonica</i>		x			S
F. Hiatellidae					
<i>Hiatella solida</i>	x	x			A
F. Gastrochaenidae					
<i>Gastrochaena carcellessi</i>		x			R
F. Crasatellidae					
<i>Crasinella lunulata</i>		x			A
<i>Crassinella marplatensis</i>		x			S
F. Myidae					
<i>Sphenia hatcheri</i>				x	A
Class Gastropoda					
F. Caecidae					
<i>Caecum antillarum</i>		x			S
Class Polyplacophora		x			S
Phylum Annelida					
Class Oligochaeta		x			S
Class Polychaeta					
Family Eunicidae					
<i>Eunice argentinensis</i>		x	x		A
<i>Marphysa aff. gallucci</i>		x	x		R
F. Lumbrineridae					
<i>Lumbrineris tetraura</i>		x	x		V
F. Phyllodocidae					
<i>Steggoa sp.</i>				x	V
F. Polynoidae					
<i>Halosydnella australis</i>		x	x		V
<i>Harmothoe sp.</i>		x	x		S
<i>Admetella?</i>		x	x		A
F. Hesionidae					
genus and species indeterminate		x			A
F. Cirratulidae					
<i>Dodecaceria sp</i>				x	V
genus et species indeterminate				x	V

Table II. – (continued)

F. Flabelligeridae				
<i>Pherusa</i> cf. <i>laevis americana</i>			x	A
F. Terebellidae				
<i>Thelepus plagiotoma</i>			x	V
<i>Thelepus?</i> sp.			x	A
<i>Pista</i> sp.			x	S
F. Chrysopetalidae				
genus et species indeterminate	x			A
<i>Paleanotus</i> sp.	x			V
F. Syllidae				
<i>Typosyllis</i> sp.	x	x		A
<i>Odontosyllis</i> sp.	x	x		S
genus et species indeterminate	x			V*
F. Sabellariidae				
<i>Sabellaria bellis</i>	x		x	A
F. Sabellidae				
<i>Potamilla</i> sp.	x			A
<i>Potamilla</i> cf. <i>platensis</i>	x			V
genus et species indeterminate 1	x			A
genus et species indeterminate 2	x			S
F. Serpulidae				
<i>Hydroides plateni</i>	x		x	V*
<i>Hydroides</i> sp. 1	x			A
<i>Hydroides</i> sp. 2	x			R
F. Spionidae				
<i>Polydora</i> sp.		x		V
<i>Polydorella</i> sp.		x	x	R
Phylum Bryozoa				
<i>Aetea anguina</i>	x		x	V*
<i>Celleporella hyalina</i>	x			V
<i>Electra monostachys</i>	x		x	V
<i>Conopeum reticulum</i>	x			V
<i>Alcyonidium</i> sp.	x			A
Phylum Echinodermata				
Class Ophiuroidea				
<i>Ophiothrix angulata</i>		x		S
gen. et sp. indet.		x		S
Phylum Chordata				
Class Ascidiacea				
<i>Corella</i> sp.	x		x	V

Mollusca, 5 of Bryozoa and 3 of Decapod crustacean.

The feeding habits of polychaetes living in *Phyllochaetopterus socialis* mats and in the benthic muddy habitat can be compared. In *P. socialis* mats, the predaceous families represented 40%, the filter-feeder 29%, and the surface deposit-feeder 29% of the total polychaetes found. In those habitats without *P. socialis*, the carnivore/motile or discretely motile guild represented 50%, and the surface deposit feeder/motile or sessile guild the other 50% of the benthic polychaete families (Roux & Bremec 1996). The apparition of filter-feeder polychaetes in the *P. socialis* mats reflects a larger complexity of the habitat, which provides a suitable and protected habitat for early juvenile development.

According to Nalesso *et al* (1995) the presence of organisms belonging to different trophic level (e.g. the polychaetes in this study) suggests that the community living between the tubes has a complex food web. In fact, this web is more complex than in

the soft bottom communities outside the aggregates.

The mollusc species registered in the Rio de la Plata muddy bottom by Roux & Bremec (1996) are different from that associated with *Phyllochaetopterus socialis*. Here, in mats, the most abundant molluscs were Mytilidae that lived attached to the tubes, to the hard basal substrate or buried in it; Roux & Bremec (1996) found only soft-bottom bivalves. On the other hand, the presence of abundant specimens of the bivalve *Hiatella solida* between the tubes is remarkable. The relationship between larvae and adults of members of Hiatellidae and the *Phyllochaetopterus* mats has been well studied in Puget Sound, Washington (Cooper & Pease 1988). These authors found evidence that a chemical induction of settlement exists for the larvae of the geoduck clam *Panope* (Hiatellidae) and that this induction is originated in the chaetopterid mats. Although *Hiatella* is able to bore into relatively soft rocks, individuals unable to find a suitable spot for penetration, can survive without boring as was observed during this study (Moore & Teichert 1969).

Table III. – *Phyllochaetopterus socialis*. Previously recorded habitat of some macrofaunal species found in aggregates. (*) infaunal habitat.

	Species	hard bottom	soft bottom	ref.
Hydrozoa	<i>Sertularella striata</i> .	rocky shores, epibiont of Hydrozoa		Genzano G. personal communication Orensanz, 1974
Polychaeta				
Eunicidae	<i>Eunice argentinensis</i>	Mytilus bed	-	
	<i>Marphysa aff. gallucci</i>	under stones, limestone	-	Orensanz, 1990
Lumbrineridae	<i>Lumbrineris tetraura</i>	Mytilus bed, crevices, algal beds	-	Orensanz, 1990
Phyllodocidae	<i>Steggoa</i> sp.	Mytilus bed	-	Orensanz, 1974
Polynoidae	<i>Harmothoe</i> sp.	Mytilus bed, <i>Macrocystis</i> beds	-	Orensanz, 1974
Cirratulidae	<i>Dodecaceria</i> sp.	<i>Macrocystis</i> beds	-	Orensanz, 1974
Terebellidae	<i>Thelepus plagiostoma</i>	under stones, cobbles, algal mats	sand	Orensanz, 1974
Chrysopetalidae	<i>Paleanotus</i> sp.	limestone	coarse sand	Orensanz, 1974
Syllidae	<i>Typosyllis</i> sp.	cobbles	-	Orensanz, 1974
Sabellariidae	<i>Sabellaria bellis</i>	rocky shores, limestone	sand	Lana & Bremec, 1994
	<i>Potamilla cf. platensis</i>	-	sand, gravel	Hartmann, 1953
Serpulidae	<i>Hydroides platani</i>	stones, limestones, mollusks shells		Zibrowius, 1971
Sipuncula	<i>Themiste petricola</i>	limestone (*)	-	Amor <i>et al.</i> , 1991
Crustacea				
Cirripedia	<i>Balanus improvisus</i>	rocky shores, limestone	-	Spivak & L'Hoste, 1975
Decapoda	<i>Pachycheles haigae</i>	rocky shores, limestone	-	Boschi <i>et al.</i> , 1992
	<i>Pachycheles chubutensis</i>	rocky shores, limestone	-	Boschi <i>et al.</i> , 1992
	<i>Pilumnus reticulatus</i>	rocky shores, limestone	-	Boschi <i>et al.</i> , 1992
Bivalvia				
Mytilidae	<i>Mytilus edulis platensis</i>	rocky shores, limestone	-	Castellanos, 1967
	<i>Musculus viator</i>	limestone	-	Castellanos, 1967
	<i>Lithophaga patagonica</i>	limestone *	-	Amor <i>et al.</i> , 1991
	<i>Brachydontes</i> sp.	rocky shores, limestone	-	Penchaszadeh, 1973
Lyonsidae	<i>Lyonsia patagonica</i>	-	sand	Castellanos, 1967
Hiatellidae	<i>Hiatella solida</i>	rocky shores, limestone	-	Castellanos, 1967
Gastrochaenidae	<i>Gastrochaena carcellessi</i>	Mytilus bed	-	Castellanos, 1967
Myidae	<i>Sphenia hatcheri</i>	rocky shores, limestone	-	Castellanos, 1967
Gastropoda				
Caecidae	<i>Caecum antillarum</i>	-	sand	Ríos, 1994

The bryozoan fauna of the Rio de la Plata estuary has been scarcely studied (López Gappa, pers comm). The species found in *Phyllochaetopterus socialis* mats have wide geographical distributions. *Celleporella hyalina*, *Electra monostachys* and *Conopeum reticulum* live in shallow coastal Argentine waters (Bremec 1990). *Aetea anguina* has been detected in coasts and continental shelf of southern Patagonia (Lopez Gappa & Lichtschein 1990); this is the first record for the Rio de La Plata area. It is a cosmopolitan species.

European, Floridean and Brazilian sabellarid worm reefs (*Sabellaria alveolata*, *S. nanella* and *Phragmatopoma lapidosa*) (Gore *et al.* 1978) support a diverse decapod crustacean fauna, that always includes a filter-feeder crab (porcellanid), a carnivore crab (usually a xanthid, sometimes *Pilumnus* spp.), and an omnivore crab (either a grapsid or pagurid). Although not highly diverse, the decapod crustaceans found in *P. socialis* mats also includes two porcellanid (*P. haigae* and *P. chubutensis*) and a xanthid (*Pilumnus reticulatus*).

The echinoderm fauna that lives in *Phyllochaetopterus socialis* is more diverse and abundant in North Carolina (USA) and Sao Paulo (Brazil) (Gettleson *et al.* 1985, Nalesso *et al.* 1995) than in the Rio de la Plata.

In this paper we extend the known distribution range for some polychaete species. Some of the indeterminate species, from several families, are probably new for the Rio de la Plata region. *Marphysa* aff. *gallucci*, *Steggoa* sp., *Harmothoe*, *Pista* sp., *Odontosyllis* sp., *Typosyllis* sp. were registered previously for the Magellanic Province but not for the Argentine Province. Meanwhile *Polydorella* sp., *Pherusa* cf. *laevis americana*, an indeterminate Chrysopetalidae, *Admetella* (?) sp. and *Sabellaria bellis* have not been cited for both biogeographical regions (Orensanz 1974, Bremec comm. pers., Bremec 1990). The previous southernmost record of *Sabellaria bellis* was Santa Catarina island, Brazil (Lana & Bremec 1994).

Table IV. – *Phyllochaetopterus socialis*. Trophic guilds of some polychaete species found in two mats (#1 and #2). B: subsurface deposit-feeder; C: carnivore; F: filter-feeder; H: herbivore; S: surface deposit-feeder; D: discretely motile; M: motile; S: sessile; J: jawed; P: pumping; T: tentaculate; X: other structures, usually eversible sac-like pharynges; n: number of specimens.

Family	Species	#1		#2		Guild
		n	%	n	%	
Hesionidae	genus and species indeterminate	-	-	7	0,93	?MJ
Lumbrineridae	<i>Lumbrineris tetraura</i>	11	4,07	6	0,80	BMJ
Phyllodocidae	<i>Steggoa</i> ?	-	-	19	2,54	CMX
Polynoidae	<i>Halosydella australis</i>	4	1,48	6	0,80	CD?J
	<i>Harmothoe</i> sp.	-	-	2	0,27	CD?J
	<i>Admetella</i> ? sp.	-	-	1	0,13	CD?J
Cirratulidae	<i>Dodecaceria</i> sp.	-	-	43	5,74	SST
	genus and species indeterminate	-	-	35	4,67	SST
Flabelligeridae	<i>Pherusa</i> cf. <i>laevis</i> americana	1	0,37	8	1,07	SDT
Terebellidae	<i>Thelepus plagiostoma</i>	27	10,00	19	2,54	SST
	<i>Pista</i> sp.	1	0,37	-	0,00	SST
Chrysopetalidae	genus and species indeterminate	4	1,48	4	0,53	CMX
Syllidae	<i>Paleonotus</i> ? sp.	-	-	9	1,20	CMX
	genus and species indeterminate	3	1,11	435	58,08	CMJ
Sabellaridae	<i>Sabellaria bellis</i>	-	-	1	0,13	FST
Sabellidae	<i>Potamilla</i> sp.	2	0,74	1	0,13	FST
	<i>Potamilla</i> cf. <i>platensis</i>	1	0,37	26	3,47	FST
	genus and species indeterminate 1	3	1,11	1	0,13	FST?
	genus and species indeterminate 2	-	-	2	0,27	FST?
		-	-	-	-	-
Serpulidae	<i>Hydroides platani</i>	212	78,52	65	8,68	FST
	<i>Hydroides</i> sp.1	-	-	5	0,67	FST
	<i>Hydroides</i> sp.2	1	0,37	-	0,00	FST
Spionidae	<i>Polydora</i> sp.	-	-	53	7,08	SDT?
	<i>Polydorella</i> sp.	-	-	1	0,13	SDT?
TOTAL		270	100,00	749	100,00	

Biogenic structures provide shelter against predation and food resources to many marine and estuarine organisms due to their structural complexity, and have an important role in the organization of tropical and temperate communities (Menge & Lubchenko 1981). The role of polychaete aggregates as shelters for soft-bottom invertebrates was described for *Diopatra cuprea* (Onuphidae) (Woodin 1978, 1981). However Luckenbach (1987) demonstrated that this species can increase post-settlement mortality of an infaunal bivalve because it provides a shelter for its predators. *Filograna implexa* (Serpulidae) (Heck & Hambrook 1991), *Phyllochaetopterus socialis* (Nalesso *et al.* 1995), *Phragmatopoma lapidosa* (Sabellaridae) (Gore *et al.* 1978, Pinheiro *et al.* 1997) and *Ficopomatus enigmaticus* (Serpulidae) (Luppi 1999) serve as refuges for hard-substrate invertebrates. The recruitment success of brachyuran and porcellanid crabs in *F. implexa*, *P. socialis*, *P. lapidosa* and *F. enigmaticus* reefs seems to be related with refuge availability (Gore *et al.* 1978, Felder & Chaney 1979, Heck & Hambrook 1991, Pinheiro *et al.* 1997, Luppi 1999). On the other hand, *Sabellaria alveolata* reefs have a key role in the development of a polychaete community pro-

viding the necessary habitat structure (Porras *et al.* 1996). The presence of juvenile polychaetes (syllids, chrysopetalids), juvenile molluscs (hiatellids and mytilids) and decapod crustacea (*Pilumnus reticulatus*, *Pachycheles haigae* and *P. chubutensis*) living in *Phyllochaetopterus socialis* aggregates supports the idea that they act as refuges for recruits of different invertebrates as well as for adult crabs and crab-like decapods.

Most of the species found in mats of *Phyllochaetopterus socialis* are benthic invertebrates which live in hard-substrates (Table III) but not in the sandy-bottom surrounding communities. However, none of them are restricted to the aggregates. These pattern of colonization was also observed in *P. socialis* mats from southern Brazil (Nalesso *et al.* 1995) and in coralligenic aggregations (Laubier 1966). The *P. socialis* mats studied here were collected offshore Punta del Este, Uruguay. The coast in that area is characterized by sandy beaches separated by rocky points. An available list of macrobenthic species from Gorriti and Lobos islands, the nearest hard substrata communities to the sampling sites (80 km), includes 4 polychaetes (some other specimens were identified at

the family level), 8 bivalves, 5 gastropods, 2 cirripedia, 3 crabs, 1 asteroid and 1 bryozoa, among other invertebrates (Riestra & Defeo 2000). From these species, only *Musculus viator*, *Brachydontes* spp., *Pilumnus reticulatus* and the cosmopolitan barnacle *Balanus improvisus* were found in *P. socialis* aggregates. Unfortunately, the intertidal and subtidal polychaete fauna of southern Uruguay rocky shores is poorly known and comparisons with mats of *P. socialis* polychaete fauna were not possible.

Many questions remained unsolved due to the lack of studies on the invertebrate fauna in this area. What is the abundance of the mats? How are colonized these mats? Does colonization involve the settlement of planktonic larvae, trapped in the mats, or the recruitment of juveniles or adults during a vagrant period of their lives? On the other hand, two other points to develop in the future will be the observation of fauna on mats at different stages of development and the sampling of water in order to identify forms of dissemination. Future research dealing with these and other aspects could elucidate the role of *Phyllochaetopterus socialis* mats in the recruitment pattern of the species living in this assemblage and the impact of a more complex community structuring and stabilizing an estuarine ecosystem.

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CONTRIBUTIONS TO THE RUNCINIDAE. I. SIX NEW SPECIES OF THE GENUS *RUNCINA* (OPISTHOBRANCHIA CEPHALASPIDEA) IN THE MEDITERRANEAN

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RUNCINA
OPISTHOBRANCHIA
MEDITERRANEAN
RADULA
ORAL ARMATURE
SEM

ABSTRACT. – Six new species of *Runcina* Forbes & Hanley, 1853, are described in this first part of a bipartite article on the Runcinidae, three more will follow in the second part (in press). All but one species are described with live coloration, radula and jaws examined by SEM. Five *Runcina* in this report are from *Posidonia/Zostera* of Banyuls-sur-Mer, France, one from the sand intersticium of Naples, Italy. *Runcina langei* n. sp. is greenish with fine dark green specks, the notum with six paired dark marginal marks and few deep black blotches, a white cross-band behind the eyes and a white rear. *R. kressae* n. sp. is yellowish with three black spotted cross lines, a white cross-band behind the eyes and a white notum rear. *R. hansbechi* n. sp. is covered densely with large, variably shaped, amoeboid black blotches, interspersed with white spots, on a yellowish ground colour. *R. nivale* n. sp. out of the mesopsammon is transparent whitish with very large eyes and gills. *R. banyulensis* n. sp., with exceptionally large eyes, is light beige with small black spots, the notum broadly bordered with white, interspersed with red and brown spots, and bearing a pure white 'T'. *R. avellana* n. sp. is chocolate brown with a lighter foot sole, one blackish brown mark on the clear tail, and clear head sides and front. A morphological introduction to the Runcinidae with emphasis on jaws and radula is given. Dental metamorphosis is observed and reanalysed.

RUNCINA
OPISTHOBRANCHIA
MEDITERRANÉE
RADULA
ARMATURE BUCCALE
SEM

RÉSUMÉ. – Six nouvelles espèces de *Runcina* Forbes & Hanley, 1853 sont décrites dans la première partie d'un article sur les Runcinidae qui se compose de deux parties ; 3 autres espèces seront décrites dans la seconde partie. La couleur sur le vivant est indiquée pour toutes les espèces, la radula et les mâchoires sont examinées au microscope électronique à balayage. Cinq *Runcina* de Banyuls/Mer (France) vivent sur *Posidonia* et *Zostera*, une espèce provient du sable interstitiel de Naples (Italie). *Runcina langei* n. sp. est verte tachetée de vert sombre, le notum montre 6 empreintes marginales, paires et sombres et quelques profondes marbrures noires, une bande transversale blanche derrière les yeux et une extrémité arrière blanche. *R. kressae* n. sp. est jaunâtre avec 3 rangées transversales de points noirs, une bande transversale à l'arrière des yeux et la partie distale du notum blanche. *R. hansbechi* n. sp. est densément couverte de larges marbrures noires à la forme amiboïde variable, interrompues de points blancs sur fond jaune. *R. nivale* n. sp., provenant des interstices du sable, est transparente, blanchâtre, avec des yeux et des branchies de forte taille. *R. banyulensis* n. sp., pourvue de grands yeux de taille exceptionnelle, est beige clair avec de petits points noirs, un notum marqué d'une large bordure blanche interrompu par des points rouges et bruns et d'un T blanc pur. *R. avellana* n. sp. est brun chocolat, avec une semelle pédieuse plus claire, une marque brun-noir sur la queue claire, et les côtés de la tête et le front clairs. L'introduction sur la morphologie des Runcinidae porte en particulier sur les mâchoires et la radula. La métamorphose des dents est observée et réanalysée.

To the late T.E. Thompson

INTRODUCTION

Runcina Forbes & Hanley, 1853, belongs to the marine euthyneuran gastropods, the Opisthobranchia. Unlike Franc (1968) who created a separate order Runcinacea we agree with Burn (1963), Ghiselin (1963), Baba (1967), Marcus & du Bois-Reymond (1970), Kress (1977), Schmekel (1985), Thompson & Brodie (1988), Gosliner (1990, 1991), Cervera *et al.* (1991) and Mikkelsen (1993, 1996), that the Runcinacea should be retained as a suborder within the Cephalaspidea. Most *Runcina* are small animals with a very characteristic colour and shape. We describe nine new species from Banyuls and Naples, six in this publication and three in the following work (Schmekel & Cappellato 2002 in press). They all belong to the genus *Runcina*. In part II the reader will find a redescription of *R. coronata* (Quatrefages, 1844) from the locus typicus, and an account of Mediterranean *R. adriatica* Thompson, 1980, *R. africana* Pruvot-Fol, 1953, *R. brenkoe* Thompson, 1980, and *R. ferruginea* Kress, 1977, all with SEM analyses of radula and jaws, to render these established species comparable with our new ones.

In the **Runcinacea** (Odhner, 1939) the dorsum is not divided transversely into two shields, the foot is undivided and without lateral extensions or parapodia. The position of the anus is terminal under the posterior mantle, (often) median or slightly to the right of the median line. The branchiae are small and positioned around or to the right of the anus, or absent. An outer (*Ildica* Bergh, 1889) or inner rudimentary shell may be present. It is mostly absent in *Runcina* Forbes & Hanley, 1853, *Runcinella* Odhner, 1924, *Runcinida* Burn, 1963 and *Ilbia* Burn, 1963. When present the inner shell is haliotiform, very fragile, small and terminal in position. There are no cephalic tentacles; oral tentacles are present only in *Ildica*. Jaws (oral armature) are present. The adult radula has in each row a broad rachidian tooth and one or two pairs of lateral teeth. Obsolete teeth are discarded and not retained in a special sac. A grinding gizzard containing four equal plates is present in most genera (not in *Ilbia* Burn, 1963 or *Pseudoilbia* Miller and Rudman, 1968). An operculum is lacking even in the embryonic stage. The euthyneurous nervous system forms a ganglionic ring with fused cerebropleural ganglia posterior to the buccal mass (Marcus & du Bois-Reymond Marcus, 1970). The common genital orifice lies often one third of the body length anterior to the anus, in the right mantle furrow, or adanal (rarely). There is an open seminal groove leading to the adoral male opening, situated on the right side, with retractile penis, prostate gland and seminal vesicle. The anterior pallial ectodermal genital organs are monaulic.

For more detailed subdivision of this group two proposals were brought forward by Burn (1963) and Baba (1967) (compare Kress 1977). Baba (1967) retains one large family, which contains all genera – Burn (1963) proposes two families: the Ildicidae and the Runcinidae. We, for the present, follow Burn (1963) like Thompson & Brodie (1988), Gosliner (1991) follows Baba (1967).

The **Runcinidae** (Burn, 1963) are without an external shell, without or with a rudimentary inner shell; without (seldom) or with up to four gills. The gills are on the right side of the anus or around it; they may be plates or plumes. The radular formula is 1.1.1 (most species) or 2.1.2. The rachidian teeth are uni- or bicuspidate (bilobed) or may be reduced. In most species they bear two pads with denticles. The laterals are hooks with smooth or denticulate cutting edges. The oral cuticula is smooth or may have jaws. The common genital pore is adanal (*Runcinella*) or more anterior (most species), one third of the body length anterior to the anus. Currently there are six genera: *Runcina* Forbes & Hanley, 1853; *Metaruncina* Baba, 1967; *Runnica* Miller & Rudman, 1968; *Runcinella* Odhner, 1924; *Runcinida* Burn, 1963; *Ilbia* Burn, 1963; *Pseudoilbia* Miller & Rudman, 1968. Thompson & Brodie (1988) are of the opinion that the genus *Runnica* is synonymous with *Runcina*.

Genus *Runcina* Forbes & Hanley, 1853 (p. 611-612):

The type species is *Pelta coronata* Quatrefages, 1844 (see description part II, Pl. 3). The name *Pelta* was suppressed in 1967 (compare Lemche 1965; Opinion 811, 1967, Bull. Zool. Nomencl. 24 (2): 89-90), and *Runcina* again became the valid name. There are up to four separate gills, close to the posteriorly placed hyponotal anus. In most species the gills are rounded plates on the right side of the anus. *Runcina coronata* and most other species are without internal shell. The radular formula is 1.1.1, median teeth are bilobed with denticles, laterals are smooth or denticulate. The common genital orifice is in the type species one third of the body length anterior to the anus. The male genital apparatus (opening adorally) has a penis and two vesicles: prostate gland and seminal vesicle. There may be an opaline gland.

Recently there have been many new descriptions of *Runcina* species in the eastern Atlantic and the Mediterranean: *R. ferruginea* Kress, 1977; *R. adriatica* Thompson, 1980; *R. brenkoe* Thompson, 1980, *R. zavodniki* Thompson, 1980; *R. aurata* Garçía, López, Luque & Cervera, 1986; *R. lenticula* Gofas, Ortea & Rodríguez, 1991; *R. macrodenticulata* Garçía, Garçía-Gómez & López de la Cuadra, 1990; *R. paupera* Ortea, Rodríguez & Valdés, 1990; *R. falciforme* Ortea, Rodríguez & Valdés, 1990; *R. bahiensis* Cervera, Garçía-Gómez & Garçía, 1991. Thompson & Brodie (1988) review the Mediterranean species and genera and summarise the diagnostic features of the world's species of *Runcina*. Kress (1977), Gosliner (1991) and Cervera *et al.* (1991) give us very helpful tables. Table I (Part II: Schmekel & Cappellato, 2002) lists the main features of the new and the already established species in the Mediterranean and the eastern Atlantic reported in the two parts of this article. In part II (Schmekel & Cappellato, 2002) a synop-

sis summarizes the characteristic features of the world's species of Runcinacea.

The morphology of the Runcinidae

Because the anatomy of this family is scarcely known, we here provide an extensive morphological account of the organs relevant to the description of the species in this study. The basic organisation of the Runcinidae (Burn, 1963) has been well analysed by Odhner 1924, Baba 1967, Ghiselin 1963, and Kress 1977.

In this family 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, and the terminal and median anus. Mikkelsen (1996) recently developed the first cladistically generated, testable morphology-based phylogeny for cephalaspids. One of the best known species is *Metaruncina setoensis* (Baba, 1954). We know its anatomy (Baba 1967, Ghiselin 1963), its embryology (Baba & Hamatani 1959), and its feeding habits (Ghiselin 1963). In *R. ferruginea* Kress, 1977, and partly in *R. coronata* (Quatrefages 1844) we know much about the fine structure: spermatophores (Kress 1985 a); male copulatory apparatus (Kress 1985 b); female genital glands of the oviduct (Kress & Schmekel 1992); digestive gland (Kress *et al.* 1994).

Ectoderm and exterior morphology: the notum may be oval (Pl. III a) or violin-shaped (Pl. II e) or more or less square (Pl. III f). The anterio-lateral border of the mantle is often somewhat enlarged and raised (Pl. I b, m), which is called 'head lobes' by us. The notum is mostly smooth or may bear weak tubercles. There may be very small oral bulbs (Pl. I b). Foot sole and notum often are more or less equal in size, but sometimes the foot sole slightly extends the notum (Pl. II l). The mantle furrow is mostly narrow (Pl. I b), sometimes broad (Pl. I a). In the right mantle furrow we find: in a median anterior position the mouth (Pl. I b), adorally the penis-opening (Pl. I d) and the seminal groove running towards the common genital pore (Pl. I a, II/3 a). In *Runcina* Forbes & Hanley, 1853, the common genital aperture lies one third from the posterior end, in *Runcinella* Odhner, 1924, it lies adanal. Near the anus there often is an opaline gland of unknown function. Peters (1993) did not find a Hancock organ with SEM + TEM studies. The left mantle furrow is without characteristic structure even in our SEM analyses. The size (Pl. I d, part II) and position (Pl. I c, part II) of the eyes vary, according to species and age.

The ground colour results from the combination of the transparent epithelium and of the hemolymph liquid. The gonad and the midgut gland themselves (viscera) mostly are pigmented. In most species the coloration and pattern are very constant (e. g. *R. hornae* Schmekel & Cappellato, in press, Pl. I c, part II), *R. brenkoae* Thompson, 1980, Pl. III a) – on the other hand there are species which are very variable (*R. langei* n.sp., Pl. IV e; *R. kressae* n. sp., Pl. III d; *R. africana* Pruvot-Fol, 1953, Pl. I, e, f, part II; compare Cervera *et al.* 1991). Within many species the opaque white pattern is more constant

and more characteristic than the dark one. The position of the black "pigment" may be species characteristic, but some details occur in more than one species; e.g. the dark marks on the base of the tail appear in *R. langei* (Pl. IV e), *R. hornae*, *R. banyulensis* n.sp., *R. kressae* (Pl. III d), and *R. elongata* n.sp. (in press), and the opaque white cross band behind the eyes occurs in *R. adriatica* (Pl. III e, f), *R. kressae* (Pl. III d), *R. banyulensis* (Pl. IV f), *R. langei* (Pl. IV e).

Shell: *Ildica* Bergh, 1889 (Curaçao, perhaps partly digested; not refound) has an adult external shell. Du Bois-Reymond-Marcus & Marcus (1963) and Marcus & du Bois-Reymond Marcus (1970) describe their adult *Lapinura divae* with a small external larval shell. Clark (1984, Bermudas) found a population of probably this species but only one third of the adult animals have a minute veliger shell (0.2 mm). We did not find an internal shell in serial sections and after NaOH maceration of *R. coronata*, *R. ferruginea*, *R. adriatica*, *R. africana*, *R. langei*, *R. kressae* and *R. hornae*. An inner shell is present in *Metaruncina setoensis* (Baba, 1954; fig. 1b: haliotiform); *Runcina australis* Burn, 1963 (Fig. 10, calcareous 0.1 mm); *R. katipoides* Miller & Rudman, 1968 (bean-shaped, Fig. 26); *Runcina marshae* Burn, 1963 (Fig. 3). Ortea & Rodríguez (1993) describe a large, dorsal, internal conjunctive plate for their *Runcinella thompsoni*. It looks very different from the shells described above.

Gills (Pl. I a, f – h, Pl. I a, e, part II, Pl. IV a, b): The gills are situated adanally in various positions (Burn 1963): They may surround the anus, be situated on both sides of it or only on the right side. The gills may consist of plumes or plates which may be subdivided (figured first by Alder & Hancock, 1846: Pl. IV, fig. 1, 5) or may be very small or absent. In all species from Banyuls they are on the right side of the anus or absent. The SEM confirms that they are rounded plates (Pl. I f), which may be subdivided (Pl. I g, h), often forming a stout whorl (Pl. I h). Depending on the direction of microscopical sections the subdivided plates may give the impression of plumes (see *R. ferruginea* Kress, 1977, fig. I D).

Oesophagus: the alimentary tract begins with the ectodermal oesophagus with the short, muscular buccal mass containing paired chitinous jaws and radula sac, followed by the gizzard with four chitinous masticatory plates.

Jaws (oral cuticular armature, Pl. VIII f, IV b, part II). The jaws (Pl. IV b) are triangular plates situated laterally. They seldom are smooth. In most of our material the SEM reveals a field of erect scales arranged densely and regularly plus one row of plates with prongs (Pl. I c). Towards the edges of the jaws and towards the gizzard the scales often are broader and less erect (Pl. VII e, g). Most of the scales are shell-shaped with one half of the "shell" slightly overlapping the other at the rim (Pl. I c, V d, e). The scales often show species characteristic differentiations: the rim may be bulgy (*R. langei*, Pl. V d) or sharp (*R. kressae*, Pl. VI g). The scales may have grooves at the rim or on their body. The grooves may (*R. hansbechi*, Pl. VII g) or may not fork (*R. langei*, Pl. V e). The pronged plates, lying flat on the matrix of the jaws, form the border facing the mouth (Pl. I c). Their processes are presumably sometimes specific in their shape (*R. africana*, Pl. V f, part II, *R. ferruginea*, Pl. VI h, part II). As preparation of the jaws is difficult, in many examined species they can only be

Plate I. – SEM micrographs of various aspects of *Runcina*. **a**, *Runcina langei* Schmekel & Cappellato, 2001, caudal right side; arrow: genital orifice, double arrow: seminal groove; **b**, *R. langei*, mouth region; F foot, arrow: small oral bulbs; **c**, *R. langei*, mouth with protruded jaws (*hyperthermic stress* method), dorsal view; P plates with prongs; S scales; **d**, *R. adriatica* Thompson, 1980, front region with protruded jaws (*hyperthermic stress* method; arrow) and penis (P); F foot; **e**, *R. africana* Pruvot-Fol, 1953, spermatophore in the notal furrow; **f**, *R. ferruginea* Kress, 1977, view onto foot surface; anus (arrow), gill with spermatophore (S) beneath it; N notum; **g**, *R. brenkoae* Thompson, 1980, caudal view, gill; note ciliary fields; F foot; **h**, *R. langei*, lateral aspect of gill; note ciliary fields; N notum.

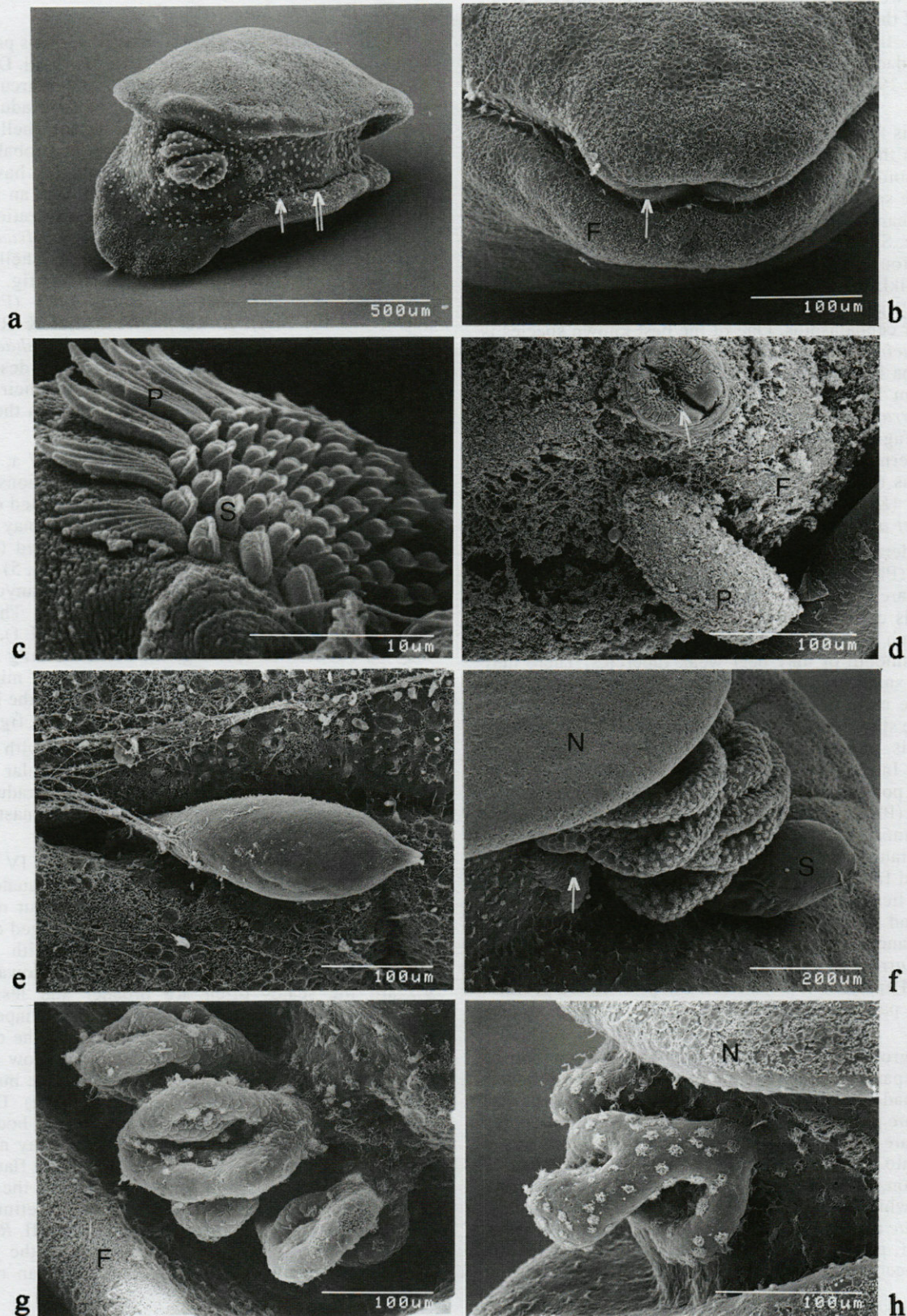
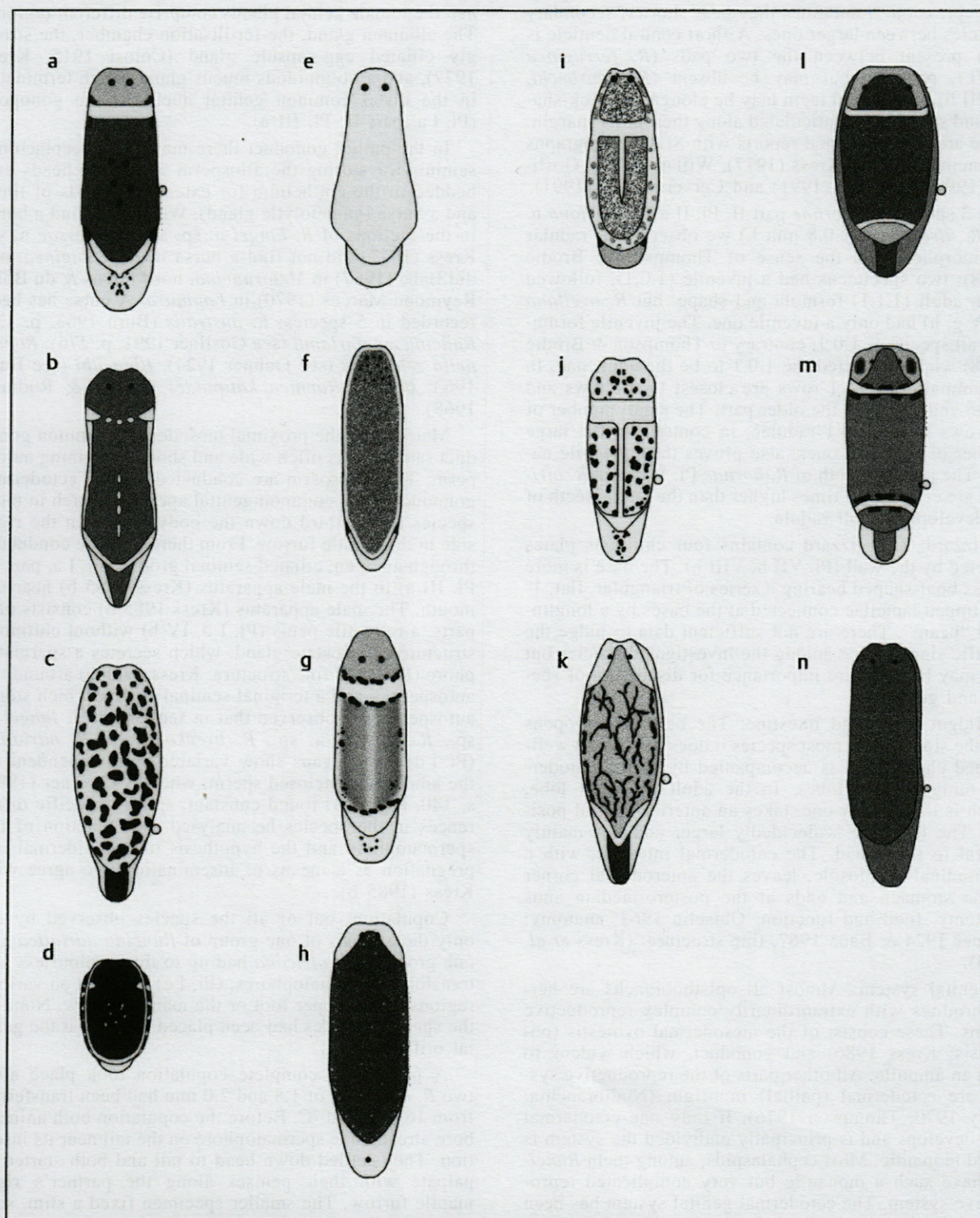


Plate II. — Schematic illustration of the new species and the known species of *Runcina* described in the two parts of this study; small circle to the animal's right indicates relative position of the genital orifice, if known. **a**, *R. langei* Schmekel & Cappellato n. sp.; **b**, *R. hornae* Schmekel & Cappellato n. sp. (description in part II, in press); **c**, *R. hansbechi* Schmekel & Cappellato n. sp.; **d**, *R. rotunda* Schmekel & Cappellato n. sp. (description in part II, in press); **e**, *R. nivale* Schmekel & Cappellato n. sp.; **f**, *R. elongata* Schmekel & Cappellato n. sp. (description in part II, in press); **g**, *R. kressae* Schmekel & Cappellato n. sp.; **h**, *R. avellana* Schmekel & Cappellato n. sp.; **i**, *R. banyulensis* Schmekel & Cappellato n. sp.; **j**, *R. adriatica* Thompson, 1980 (description in part II, in press); **k**, *R. brenkoae* Thompson, 1980 (description in part II, in press); **l**, *R. coronata* (Quatrefages, 1844) (description in part II, in press); **m**, *R. africana* Pruvot-Fol, 1953 (description in part II, in press); **n**, *R. ferruginea* Kress, 1977 (description in part II, in press).



shown from the reverse side, which is the side of secretion. When seen from the reverse side the scales are bowl- or saucer-shaped Pl. VI h, part II).

Radula: The radular formula (in press Pl. V a, part II) is usually 1.1.1 (Pl. VII a-d), seldom 2.1.2, or the radula may be reduced to several aberrantly shaped teeth in disarray (Baba 1954, Ghiselin 1963). The rachidian teeth are broadly horseshoe-shaped, seldom uni- but mostly bicuspidate (bilobed) and with denticles of variable and often species-characteristic shape on either side of a central depression. Sometimes they bear shorter, secondary denticles between larger ones. A short central denticle is often present between the two pads (*R. ferruginea* Pl. VI f, part II), but may be absent (*R. hansbechi*, Pl. VII b). The lateral teeth may be elongated, hook-shaped and smooth or denticulated along their outer margin. There are five published reports with SEM micrographs of runcinid radulae: Kress (1977), Willan (1981), Gosliner (1990), Gosliner (1991) and Cervera *et al.* (1991).

In 3 species (*R. hornae* part II, Pl. II a; *R. avellana* n. sp., *R. africana*, 0.7-0.8 mm l.) we observed a 'radular metamorphosis' in the sense of Thompson & Brodie (1988): two specimens had a juvenile (1.0.1), followed by an adult (1.1.1) formula and shape, but *R. avellana* (Pl. V g, h) had only a juvenile one. The juvenile formula in all species is 1.0.1, contrary to Thompson & Brodie (1988) who interpreted the 1.0.1 to be the adult one. In our animals the 1.0.1 rows are closest to the jaws and mouth and therefore the older part. The small number of 3-5 rows in the 1.0.1 radulae, in contrast to the large number of the adult ones, also proves their juvenile nature. The juvenile teeth of *R. hornae* Pl. V a) and *R. africana* are curiously 3 times higher than the lateral teeth of the developing adult radula.

Gizzard: The gizzard contains four chitinous plates secreted by the wall (Pl. VII h, VIII h). The base is more or less boat-shaped bearing a series of triangular, flat, 1- to 3-tipped lamellae connected at the bases by a longitudinal "beam". There are not sufficient data to judge the specific significance among the investigated species but they may be of future importance for discussion of species and genera.

Midgut gland and intestine: The oesophagus opens into the stomach. In most species it does not form a well-defined chamber. It is accompanied by paired entodermal midgut gland lobes. In the adult the right lobe, which is the smaller one, takes an anterior-ventral position. The left lobe is decidedly larger and lies mainly ventral to the gonad. The entodermal intestine, with a longitudinal typhlosole, leaves the anterodorsal corner of the stomach and ends at the postero-median anus (anatomy, food and function: Ghiselin 1963; anatomy: Odhner 1924 & Baba 1967, fine structure: (Kress *et al.* 1994).

Genital system: Almost all opisthobranchs are hermaphrodites with extraordinarily complex reproductive organs. These consist of the mesodermal ovotestis (oogenesis: Kress 1986) and gonoduct, which widens to form an ampulla. All other parts of the reproductive system are ectodermal (pallial) in origin (Nudibranchia: Tardy 1970, Thompson 1976). If only one ectodermal tube develops and is principally undivided the system is called monaulic. Most cephalaspids, among them *Runcina*, have such a monaulic but very complicated reproductive system. The ectodermal genital system has been histologically examined as far as possible in the new

species. Among the few species with abundant material available, these parts do not seem to differ much, and are similar to those of *R. ferruginea* Kress 1977. Little is known about the variability of the ectodermal genital system due to age and species.

Female ectodermal apparatus: This system is well studied in *Metaruncina* Baba, 1967, *Runcinella* Odhner, 1924, *R. coronata* (Quatrefages, 1844) and *R. ferruginea* Kress, 1977 (Kress & Schmekel, 1992). In most other species it is scarcely known or not at all. In *R. ferruginea* the female genital glands comprise different regions: The albumen gland, the fertilisation chamber, the strongly ciliated egg-capsule gland (Colosi 1915, Kress 1977), and a voluminous mucus gland which terminates in the distal common genital duct and the gonopore (Pl. I a, part II: Pl. III a).

In the pallial gonoduct there may be a receptaculum seminis for storing the allosperm with their heads embedded in the epithelium for extended periods of time, and a bursa (gametolytic gland). We did not find a bursa in the sections of *R. langei* n. sp. and *R. kressae* n. sp. Kress (1977) did not find a bursa in *R. ferruginea*, nor did Baba (1967) in *Metaruncina*, nor Marcus & du Bois-Reymond Marcus (1970) in *Lapinura*. A bursa has been recorded in 5 species: *R. australis* (Burn 1963, p. 13); *Runcina macfarlandi* (see Gosliner 1991, p. 276); *Runcinella zelandica* (see Odhner 1924), *Ilbia ilbi* (see Burn 1963, p. 18); *Runnica katipoides* (Miller & Rudman 1968).

Male ducts: the proximal mesodermal common gonoduct (ampulla) is often wide and short, containing autosperm. The autosperm are conducted via the ectodermal gonoduct to the common genital aperture, which in most species is two third down the body length on the right side in the mantle furrow. From there they are conducted through an open, ciliated seminal groove (Pl. I a, part II: Pl. III a) to the male apparatus (Kress 1985 b) near the mouth. The male apparatus (Kress 1985 b) consists of 3 parts, a retractile penis (Pl. I d, IV b) without chitinous structures, a prostate gland, which secretes a spermatophore (Pl. I e, f; fine structure: Kress 1985 b) around the autosperm – and a terminal seminal vesicle which stores autosperm. We observed that in sections of *R. langei* n. sp., *R. kressae* n. sp., *R. brenkoae* and *R. adriatica* (Pl. I d) both organs show variable sizes dependent on the amount of enclosed sperm, whereas Gosliner (1990, s. 140, Fig. 5 B) found constant, species-specific differences in the species he analysed. For function of the spermatophore and the hypothesis of subepidermal impregnation as a means of insemination, we agree with Kress (1985 b).

Copulation: out of all the species observed by us, only the animals of one group of *Runcina adriatica* and one group of *R. africana* had up to three colourless and translucent spermatophores. (Pl. I e) attached on various regions of the upper foot or the mantle furrow. None of the spermatophores had been placed directly at the genital orifice.

A probably incomplete copulation took place after two *R. adriatica* of 1.8 and 2.0 mm had been transferred from 16 °C to 20 °C. Before the copulation both animals bore already one spermatophore on the tail near its insertion. They settled down head to tail and both started to palpate with their penises along the partner's right mantle furrow. The smaller specimen fixed a slim, sausage-shaped and milky-white spermatophore ventrally

into the mantle furrow, a distance behind the genital orifice of the partner. The passing of the spermatophore could be seen through the transparent penis. Then the animals separated immediately. The copulation lasted only 2 to 3 minutes (result of artificial environment?); the spermatophore was expelled within 20 seconds. An hour later the spermatophore looked swollen, oval, taut and more transparent. Neither specimen spawned within two days after copulation.

Development: A spawn consists of few and large eggs rich in yolk (Ros 1981), e.g. in *R. coronata* (Quatrefages, 1844), *Metaruncina setoensis* (Baba, 1954), and *R. ferruginea* Kress, 1977. The development is 'direct' (intracapsular, without freely swimming veliger) in *R. coronata* (Vayssi re, 1900), *Runcinida elioti* (Baba, 1937, see Baba & Hamatani 1959), *Metaruncina setoensis*, and *R. ferruginea*. There is a remarkable study on the ontogenesis in *M. setoensis* by Baba and Hamatani (1959). We do not know if all species have such direct development. Ghiselin (1963) and Gosliner (1990) emphasised the phylogenetic value of this development type.

Though the majority of species seems to be very local (no free swimming veliger stage), in the discussion of our new species we consider all world-wide known, externally similar species.

MATERIAL AND METHODS

Schmekel collected Mediterranean runcinids in addition to Saccoglossa and Nudibranchia in Naples, Italy, 1965-1970, Portmann and Sandmeier-Fioroni 1958 at Observatoire Arago, Banyuls-sur-Mer (42 N; 3  E), France. Both authors collected intensively since 1993 at Observatoire Arago, Banyuls. *Runcina coronata* were hand-sampled from tidal pools near the upper littoral fringe in Roscoff (Bretagne, Atlantic, France) at low tide in spring 1972-74, *R. ferruginea* collected in August 1974/November 1975 by Kress in Plymouth. Almost all other species were collected at Banyuls from rhizomes of *Posidonia*, *Zostera*, *Cymodocea* or small algae, mainly by diving or dredging at 0-30 m, and some at Naples (Italy). The algae or rhizomes were left undisturbed some hours up to 2 days in bowls with seawater. Under these conditions *Runcina* spp., searching for oxygen, climb to the surface. The animals were relaxed with 7% MgCl in aqua dest. Some were fixed in 7% formaldehyde in seawater but most in acid Bouin's solution in aqua dest (Romeis, 1968, N  304, p. 73). After dehydration through an alcohol series, the specimens were retained in 70% alcohol. 1-3 specimens each of *R. hornae* n. sp. (part II, in press), *R. kressae* n. sp., *R. langei* n. sp., *R. adriatica* Thompson, 1980, *R. africana* Pruvot-Fol, 1953, *R. brenkoae* Thompson, 1980, *R. coronata* (Quatrefages, 1844), and *R. ferruginea* Kress, 1977 were analysed histologically. For light microscopy, paraffin-embedded material was serially sectioned longitudinally and transversely at 5 m. The slides were stained with May-Gr nwald-Giemsa, Hemalaun-Chromotrop and Alcianblue (Romeis 1968). For scanning electron microscopy (SEM), animals fixed in Bouin's solution were dehydrated in ethanol, critical point dried (c.p.d.) with CO₂ and coated with gold. SEM was carried out on a Hitachi S-530.

For the examination of jaws lining the pharynx in their natural position, living specimens were heated for several minutes in their small water bowl under a hot lamp. With this *hyperthermic stress* method the animals protrude their mouth and expose their jaws. The technique didn't work in all species.

All radular formulae and measurements for jaws, teeth and gizzard plates are the maximum evaluated for each species, unless otherwise noted.

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

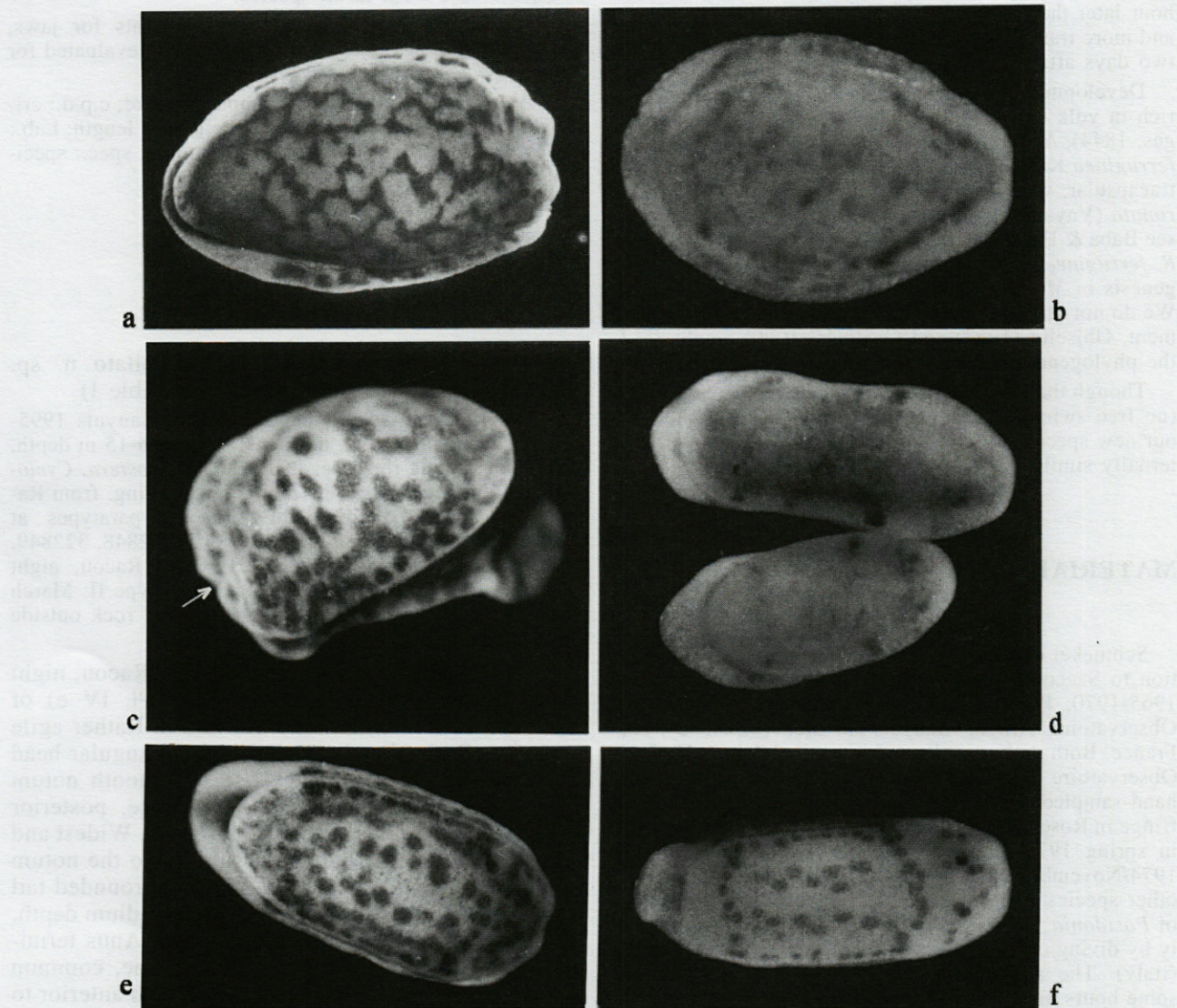
Runcina langei Schmekel & Cappellato n. sp. (Pl. II a, IV e, V, I a-c, h, part II, Table I)

Material: 180 specs., 0.5-2.0 mm l., Banyuls 1995-1997, most from 1997, none in 1998, ca. 5-15 m depth, common among rhizomes of *Posidonia*, *Zostera*, *Cymodocea*, and small algae by dredging or diving, from Racou to Cap l'Abeille; holotype and paratypes at Senckenberg Mus., Frankfurt, No SMF 322848, 322849, 322850. Paratype I: March 28th, 1996, Racou, night dredge, *Posidonia* rhizomes, 5-8 m; paratype II: March 24th, 1997, *Posidonia* rhizomes and small rock outside the Observatoire Arago at 4-8 m.

Description of the living holotype (Racou, night dredge, March 28th, 1996, 5-8 m; Pl. IV e) of 1.9 mm l., 0.5 mm w, and 0.4 mm h. Rather agile species. Body shape rounded with an angular head and distinct head lobes (Pl. II a). Smooth notum with straight or notched anterior edge, posterior notum end forming a slightly raised tip. Widest and highest part of the body just anterior to the notum end. Foot as wide as notum, long and rounded tail (0.5 mm l.). Eyes of medium size in medium depth, close to the anterior end of the head. Anus terminal, just to the right of the median line, common genital pore one third of the body length anterior to it (Pl. II a). With SEM a large spec. (1.2 mm c.p.d.), not the holotype, has 2 rounded gill laminae to the right of the anus, the smaller and undivided one more dorsal and closer to the anus, the bigger one further to the right and divided into 2 or 3 horizontal arcs (Pl. I h).

Ground colour translucent yellowish green, with a light yellow margin. Whole animal covered with fine olive green specks, typically denser around the eyes and along the notal margin. Olive green viscera visible through the notum, right above them few blackish blotches (Pl. IV e). A broad, straight band of small, round, dense, opaque white spots crosses the notum behind the eyes. Notum rear rather broadly bordered with white spots, following the outline of the notum (Pl. II a). The white cross-band and the white of the notum rear continue ventrally through the notal furrow onto the upper foot.

Plate III. – Light micrographs. **a**, *Runcina brenkoae* Thompson, 1980, adult, 2 mm length (description in part II, in press); **b**, *R. brenkoae* juv., 1 mm length (description in part II, in press); **c**, *R. hansbechi* Schmekel & Cappellato n. sp. holotype, 1.4 mm length; arrow: contracted head region; **d**, *R. kressae* Schmekel & Cappellato n. sp. fix. 0.6, 0.9 mm length (holotype); **e**, *R. adriatica* Thompson, 1980, 1.9 mm length; variety with black spots beneath the opaque white of the notum rear; **f**, *R. adriatica*, 1.6 mm length; note black blotches filed up in longitudinal and transverse lines.



Some scattered fine blackish specks along the notal margin, accumulated to form three striking, paired, marginal black marks anteriorly and posteriorly to the white cross-band behind the eyes, and anteriorly to the white notum rear (Pl. II a). Like the white cross-band, the black marks run down through the notal furrow onto the upper foot just beneath their positions, most prominent at the insertion of the tail. Translucent tail with a number of fine black specks on its centre and a border of small white spots on its sides. Foot sole greenish, without any white and black pigment. Colour varieties: this is a very variable species. The ground colour can be more greenish with a brownish-orange tinge. Viscera light green to dark olive green.

Dark marks close to the white notal areas sometimes faint on the light colour variety. White cross-band behind the eyes sometimes discontinuous. White area at the notum rear rarely absent. In some specimens the white spots are so dense that the animals appear whitish all over.

Anatomy: Jaws (Pl. V d, e) of a 1 mm (fix.) animal set with shell-shaped scales, their rims orientated transversely towards the mouth. Each rim shaped as a smooth big bulge (Pl. V e). Basal to it a couple of very fine, vertical, parallel, straight and unforked grooves on the side facing the stomach, (Pl. V d), running down about one third of the body of the scales. Towards the mouth similar grooves run through the horizontal furrow just below the

Plate IV. – Light micrographs. **a**, *Runcina nivale* Schmekel & Cappellato n. sp. holotype, 2 mm length of fixated animal, note large eyes and gills; **b**, *R. adriatica* Thompson, 1980, 1.2 mm length, after short exposure to Na OH; dotted outline: penis, arrow: jaws, double arrow: radula; **c**, *R. avellana* Schmekel & Cappellato n. sp. holotype, 1.2 mm length; **d**, *R. sp.* 0.6 mm length, green variety of *R. avellana* or n. sp. ?; **e**, *R. langei* Schmekel & Cappellato n. sp. holotype, 0.8 mm length; **f**, *R. banyulensis* Schmekel & Cappellato n. sp. holotype, 1.1 mm length, note large eyes close to the front.



bulge, but do not exceed the furrow. 9 plates (Pl. V d), three times larger than the scales, with 7-9 densely parallel and fairly pointed prongs ($1.8 \mu\text{m}$ l.).

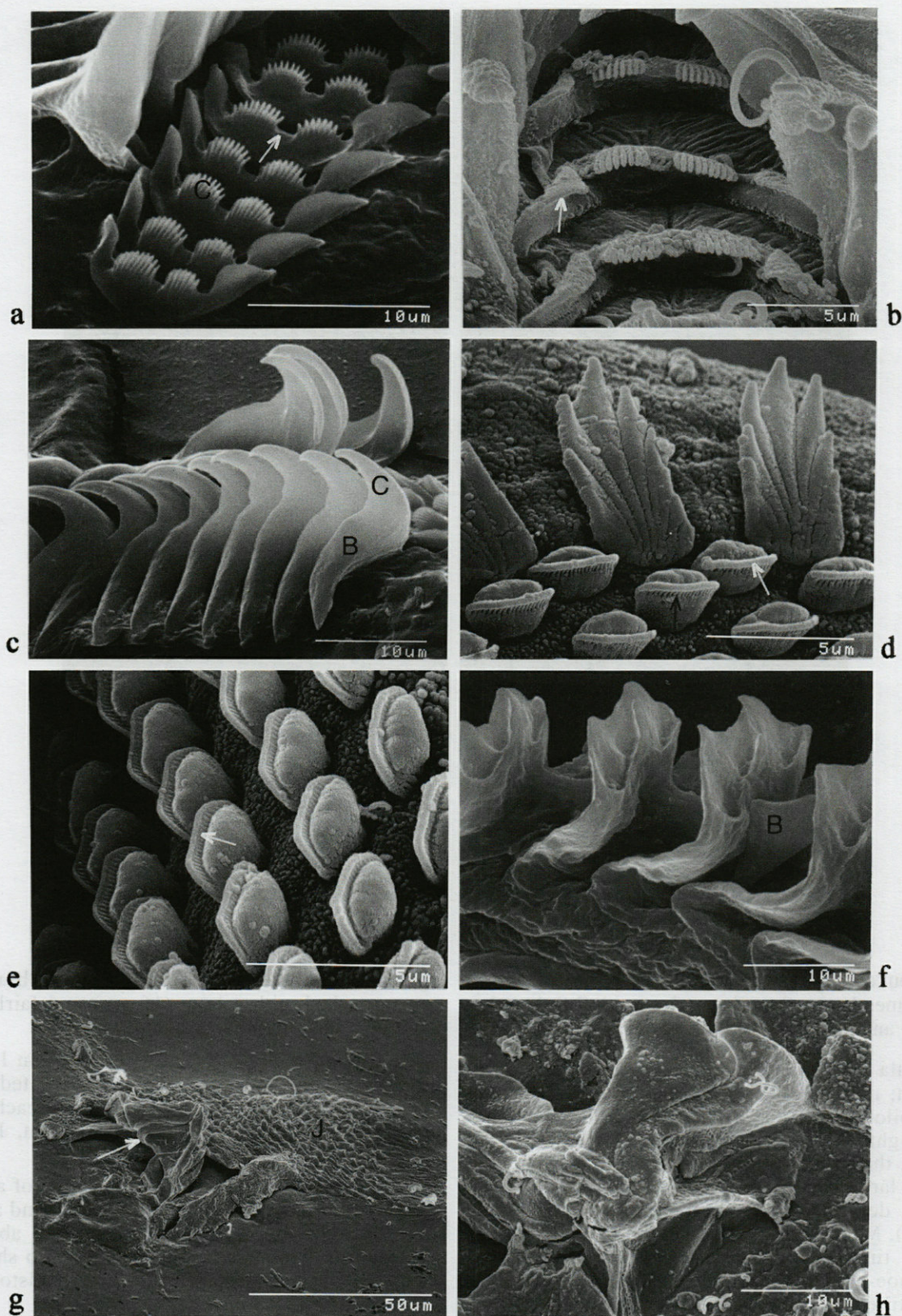
Radula (Pl. V a-c): $22 \times 1.1.1$ (spec. fix. 1.1 mm; rad. l. $130 \mu\text{m}$). Rachidian teeth ($15 \mu\text{m}$ wide) bilobed (Pl. V a, b), each pad with 6-10 slender, slightly diverging denticles of equal length ($2 \mu\text{m}$), their tips forming a slight arc, less curved on the larger teeth. Pads flatly *Cardium* shaped. Central depression deep and broad (up to $2 \mu\text{m}$; Pl. V b). Most teeth without central denticle, some with a tiny, triangular and pointed one. Bases horseshoe-shaped, sides ($10 \mu\text{m}$ l.) rather high laterally, tilted inwards, their upper edges forming an-

gular lobes. Laterals (Pl. V c) smooth, blunt and swan-necked with a long ($16 \mu\text{m}$) and fairly high ($10 \mu\text{m}$) base without a hump.

4 triangular gizzard plates ($80-100 \mu\text{m}$ l.) with one broad end and the other more pointed. They bear 8 lamellae (Pl. V f) with 1-3 tips each, their bases connected by a thick basal beam, leaving only one third of the tips free.

Male copulatory apparatus consisting of a short, wide penis, a cylindrical prostate gland and a seminal vesicle of variable size with abundant autosperm. No bursa has been found. No shell detectable by NaOH maceration nor in histological sections.

Plate V. – SEM micrographs. **a – f.** *Runcina langei* Schmekel & Capellato n. sp.; **a**, radula; C one pad of a bilobed rachidian tooth, arrow: central depression; **b**, rachidian teeth; arrow: side of rachidian tooth tilted angularly inwards; **c**, lateral teeth; B base, C cusp; **d**, jaw plates with prongs, scales with unforked furrows (black arrow), side facing the stomach; white arrow: bulge; **e**, jaw scales with unforked furrows (arrow), side facing the mouth; **f**, detail of gizzard plate; B basal beam. **g, h.** *Runcina avellana* Schmekel & Capellato n. sp. **g**, juvenile radula (arrow) and reverse side of jaws (J); **h**, juvenile radula, view from above.



Etymology. This species is named in honour of Mr. Joe Lange, University of Münster, Germany, for his masterly work at the SEM.

Discussion. For comparison with *R. kressae* Schmekel & Cappellato n. sp., see discussion there. *R. prasina* (Mörch, 1863), from the Antilles, which is light green, has its notum covered with dense, minute warts while in *R. langei* the notum is smooth. The Bermudan species *R. inconspicua* Verrill 1901-1902, with a dark green-brown notum and a thin orange margin, has a light green foot with an orange-violet, uniquely undulating margin. Such margins do not occur in *R. langei*. *R. australis* Burn, 1963 (p. 10-15, Figs 1-11), from New South Wales, a greenish-black species with an ashy-yellow margin, has a small inner shell and denticulate laterals. *R. langei* has no shell and smooth laterals. *R. adriatica* Thompson, 1980, from Rovinj, has circular, isolated black blotches often arranged in rows, while *R. langei* is covered with fine, diffuse olive-green specks, and three paired, marginal black marks at the notal margin. The scales of the jaws of both species bear grooves, but in *R. adriatica* (part II: Pl. IV c) the grooves are only on one side, in *R. langei* (Pl. V d, e) on both sides. The plates of the jaws of *R. adriatica* (part II, Pl. IV b) have blunt prongs – in *R. langei* (Pl. V d) they are more pointed. The body colour of *R. falciforme* Ortea, Rodríguez & Valdés, 1990, from Cape Verde Islands, is uniform, transparent green, while *R. langei* is covered with fine, olive green specks. The laterals of *R. falciforme* are denticulate, but smooth in *R. langei*, and the position of the genital pore is more adanal than in *R. langei*. *R. paupera* Ortea, Rodríguez & Valdés, 1990, also from Cape Verde Islands, like *R. langei*, has small black spots in the centre of the brownish-green notum. The authors did not mention any opaque white markings, abundantly present in *R. langei*. The teeth of the radula of *R. paupera* have twice the number of *R. langei* ($22 \times 1.1.1$). The cutting edge of the rachidians is straight and the laterals might have fine denticles (Ortea *et al.*, 1990, fig. 4 K, 4 L), in contrast to arced rachidian pads and smooth laterals in *R. langei*. The common genital aperture lies close to the anus only in *R. paupera*. The brown to olive-green *R. macrodenticulata* García *et al.*, 1990, from Gibraltar, has longitudinal brown, olive green and yellowish-white bands on the head, whereas *R. langei* only has one white cross-band behind the eyes. The unique giant denticles of the lateral teeth separate it clearly from *R. langei*.

***Runcina kressae* Schmekel & Cappellato n. sp.** (Pl. II g, III d, VI a-h; part II, Table I).

Banyuls: 3 specs. 0.7-2.0 mm l., Aug. 1986; 54 specs., 0.5-2.5 mm l.; 1994-1998, ca. 5-15 m depth, from rhizomes of *Posidonia*, *Zostera*, *Cymodocea* and small algae from Racou to Cap l'Abeille. Holotype and paratypes at Senckenberg Mus., Frankfurt, n° 322851, 322852.

Description of the living paratype (March 28, 1996, outside the Observatoire Arago at 5 m depth) of 1.8 mm l., 0.4 mm w., 0.3 mm h., tail 0.4 mm (holotype: Sept. 25, 1998, outside the Centre Héli-Marine, 2 m depth; Pl. III d, fix. 0.9 mm h., 0.5 mm w., 0.3 mm h., tail 0.1 mm). Very agile, crawling quickly. Body shape elongated, flat, with a fairly pointed and slightly notched anterior region. In movement there are small head lobes. Rear of the smooth notum rounded and not raised. Foot as wide as notum, tail long, rounded. Eyes of medium size, close to and slightly lateral to the buccal mass. Common genital opening one third of the body length anterior to the median anus. Gills to the right of the anus, consisting of 2 rounded laminae, the larger and more ventral one subdivided into horizontal arcs, once dorsal and three times ventral, and the smaller one a simple lamina.

Ground colour yellowish. Brownish-greenish viscera visible through the ectoderm. Notum crossed by a broad band of tiny, opaque white, round spots a short distance behind the eyes. Notum rear opaque white with an almost straight anterior outline (Pl. III d). Scattered white spots on the notum, more concentrated along the median line of the body, and bordering the lateral notum rim, here interspersed with dark patches. Rounded to oval black patches of somewhat variable size border the white cross-band and the anterior outline of the white notum rear, thus forming three striking, black transverse lines (Pl. II g, III d). Black and white cross-bands slightly curved away from the front and continuing laterally down the notal furrow onto the foot. Foot sole uniformly yellowish-greenish without any dark patches. Tail with a few blackish-brown spots in its centre close to the body, and flanked by few small white spots. **Colour varieties:** the dark patches may form less distinct cross-bands but be partially scattered may be over the notum. Rarely do they form a fourth cross-band. The tiny white spots very dense, even partly obscuring the eyes. Sometimes the foot sole is sprinkled with white spots or may bear a few dark patches, often arranged in a cross line just anteriorly to the tail. The tail may lack dark patches completely or may have more patches or streaks.

Anatomy: Triangular jaws (Pl. VI e; spec. fix. 0.8 mm) with scales shaped like a closed shell. Edge of the scales a sharp rim (Pl. VI g), below it both sides with very fine and parallel, vertical, unforked grooves. On the side facing the gizzard they run down one quarter of the scale, on the side facing the mouth they do not exceed the horizontal furrow just below the rim (Pl. VI g; spec. fix. 0.6 mm). 6-7 plates ($4 \times 8 \mu\text{m}$, tips $2.5 \mu\text{m}$ l.) with 6-11 pointed prongs each (Pl. VI f; spec. fix. 0.8 mm), arranged close together, their size decreasing strongly towards the sides of each plate.

Radula (Pl. VI a-d): $25 \times 1.1.1$ (spec. fix. 1.8 mm; rad. l. $240 \mu\text{m}$). Rachidian teeth ($16 \mu\text{m}$ w.

in the 0.8 mm spec.) bilobed (Pl. VI c) with 10-14 dense denticles of nearly equal length (1.6 μ m long, 0.4 μ m l.) per pad, forming a slightly curved, flat comb. A broad (1.0 μ m) and deep depression between the two pads. Of three examined radulae the rachidians of two lack a central denticle, in a third they bear a short one. The sides (13 μ m l. in the 0.8 mm spec.) are relatively erect and hardly tilted inwards (Pl. VI d). The laterals (21 μ m b. in a 1.8 mm spec.) are smooth, blunt and swan-necked, mostly without hump (Pl. VI a). There seems to be a distinct groove (Pl. VI b) along the backside of the cusp (19 μ m h.).

4 gizzard plates (55 μ m l., Pl. VI h) with 6 lamellae, each with 3 tips (spec. 0.8 mm). A beam connecting the bases of all lamellae leaves half of the lamellae free.

Male copulatory apparatus consisting of a short, wide penis, a cylindrical prostate gland and a seminal vesicle of variable size with a great amount of sperm. No bursa has been found. No shell detectable by NaOH maceration or in histological sections.

Etymology. This species is named in warm and thankful friendship to Dr. Annetrudi Kress, Basel, Switzerland, who provided us with many specimens of *Runcina coronata* (de Quatrefages, 1844) and *Runcina ferruginea* Kress, 1977 from Plymouth, GB.

Discussion. For comparison of this new species with *R. hansbechi* n. sp., and *R. banyulensis* n. sp., see discussions there. As there are certain external similarities between *R. langei* and *R. kressae*, these two species must be compared carefully. The body of *R. langei* is rounded with a rounded tail, while *R. kressae* is elongated with a pointed tail. *R. langei* has tiny olive green specks spread diffusely over the body and white spots only bordering the outline of the notum end. *R. kressae* has 3 striking black cross-bands and an opaque white half-moon on the notum rear, with a straight anterior border. The jaws of *R. langei* and *R. kressae* both have scales with grooves. But *R. langei* has a comfortable, smooth bulge (Pl. V d) along the rim – which is sharp in *R. kressae* (Pl. VI g). In *R. langei* the vertical grooves end below the bulge (Pl. V d), in *R. kressae* these grooves reach onto the rim of the scales itself (Pl. VI g). The sides of the rachidians are higher and less tilted inward in *R. kressae* than in *R. langei* (Pl. VI d, V b). The notum of *R. capreensis* Mazzarelli, 1894, from Capri, bears isolated, rounded black blotches spread evenly over the charcoal black notum but never arranged in cross-bands like in *R. kressae*. The circular, isolated black blotches in *R. adriatica* are spread evenly or filed up in longitudinal and transverse lines on the notum (Pl. II j, III e, f), whereas they form only three cross-bands in *R. kressae* (Pl. II g, III d). The scales of the jaws show striking differences. In *R. kressae* they have a sharp rim and grooves on both sides, in *R. adriatica* there is a

thick bulge along the rim, and grooves only on one side (part II, Pl. V c). The brown to olive green *R. macrodenticulata* Garçia *et al.* 1990, from Gibraltar, has longitudinal brown, olive green and yellowish-white bands on the head but no transverse bands like *R. kressae*. The laterals of *R. macrodenticulata* have giant denticles, but those of *R. kressae* are smooth. *R. paupera* Ortea, Rodríguez & Valdés, 1990, from Cape Verde Islands, exhibits diffuse black spots in the centre of the brownish-green notum. There are no opaque white spots or transverse bands such as in *R. kressae*. The radular formula is about twice the number of *R. kressae*. The laterals (Ortea *et al.* 1990, fig. 4L) seem to have fine denticles, but are smooth in *R. kressae*. The genital pore lies close to the anus only in *R. paupera*.

***Runcina hansbechi* Schmekel & Cappellato n. sp.** (Pl. II c, III c, VII a-h; part II, Table I)

Material: 6 specs. 0.8-2.6 mm l.: 4 $\times$ Sept. 1997, 2 $\times$ Sept. 1998. Banyuls, collected by diving from *Posidonia* rhizomes at 8 m depth outside the Observatoire Arago and from rocks with algal growth near the surface near the Centre Héli-Marine. Holotype at Senckenberg Mus., Frankfurt, N° 322853.

Description of the living holotype (March 30th, 1996; *Posidonia* rhizomes, 8 m depth outside the Observatoire Arago; Pl. III c) of 2.2 mm l., 0.6 mm w., and 0.4 mm h., tail 0.5 mm. Animal moderately agile. Body shape oval; smooth notum slightly notched anteriorly with distinct head lobes; rear slightly raised. Foot as wide as notum, tail fairly wide and rounded. Rather small eyes, relatively wide apart and difficult to distinguish among the colour pattern. Anus terminal and median, common genital opening anterior to the last third of the body. Two rounded gills, subdivided several times horizontally, to the right of the anus.

Ground colour of the body yellowish-beige. Viscera pale orange to brownish. Notum, notal furrow, foot, foot sole, and median region of the tail covered with large, amoeboid black blotches of variable shape and size (Pl. III c), often close to each other, sometimes even merging. The size of the blotches decreases towards the notal margin. On the foot sole they are less intensive but even larger than on the notum. On the upper foot they are more distinct again, resembling a string of pearls. The black blotches on the median of the tail lie within a broad band of dark brown pigment (Pl. II c). On the notum the spaces between the black blotches are covered with small, opaque white spots, thus giving the impression of sinuous lines and fields. The white spots are denser at the notal margin, with exception of the head. Sides of tail densely covered with white spots, less so the foot sole. Gills transparent with black pigment deep below the surface. **Varieties:** Two specimens from 09.1998 have very small white triangles behind the eyes on the sides of the head.

Plate VI. – SEM micrographs. *Runcina kressae* Schmekel & Cappellato n. sp.; **a**, radula; Ra rachidian teeth, L lateral teeth; **b**, lateral teeth with groove (G); **c**, rachidian teeth; arrow: broad central depression without central denticle; **d**, radula; arrow: erect sides of rachidian teeth; **e**, reverse side of jaws; S saucer shaped scales, P plates with prongs; **f**, protruded jaws (hyperthermic stress method), plates with prongs (bottom), scales (top); **g**, detail of 'f'; scales with unforked furrows and sharp rim (R); black arrow: side facing the mouth, white arrow: side facing the stomach; **h**, gizzard plate.

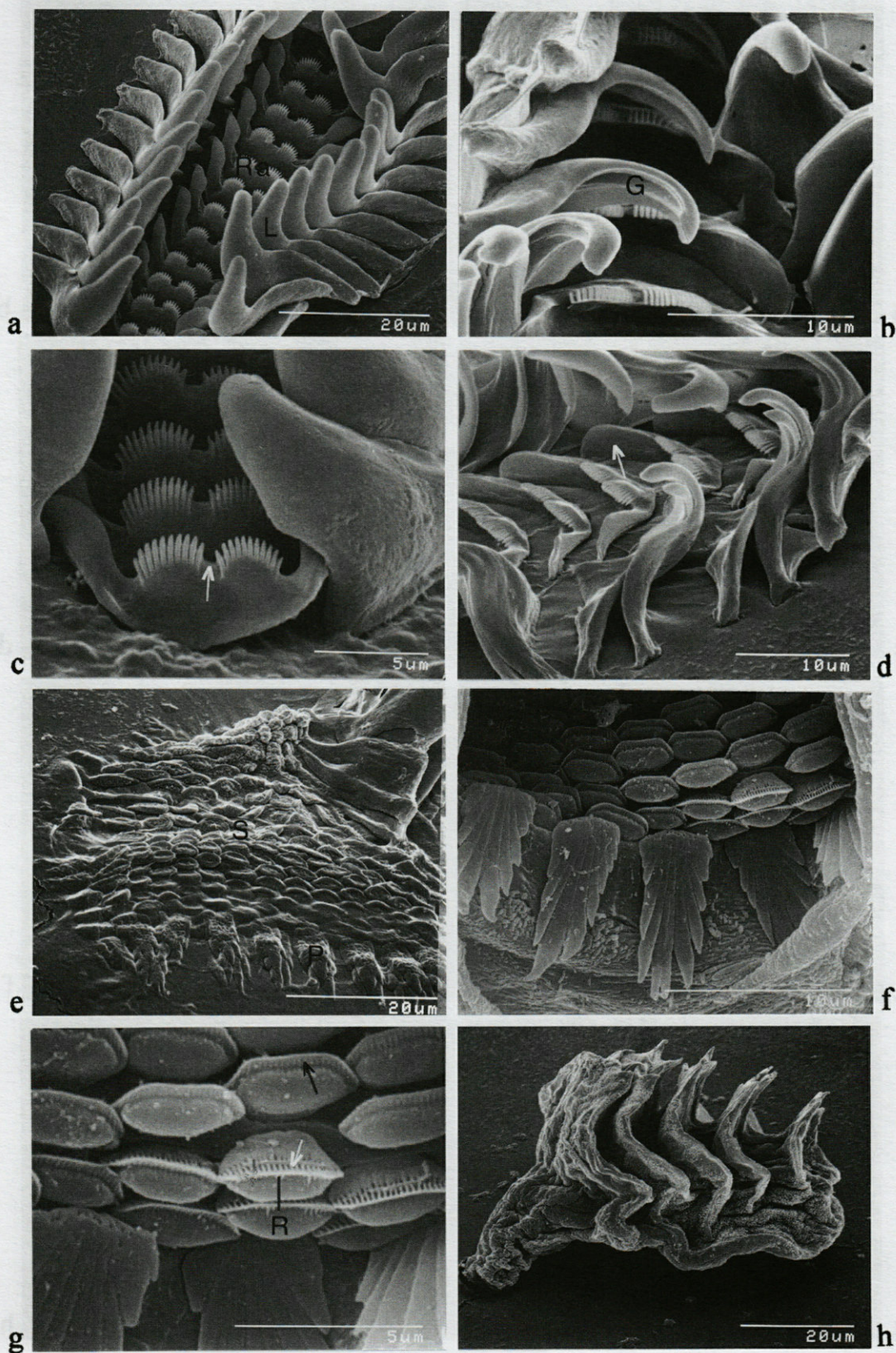
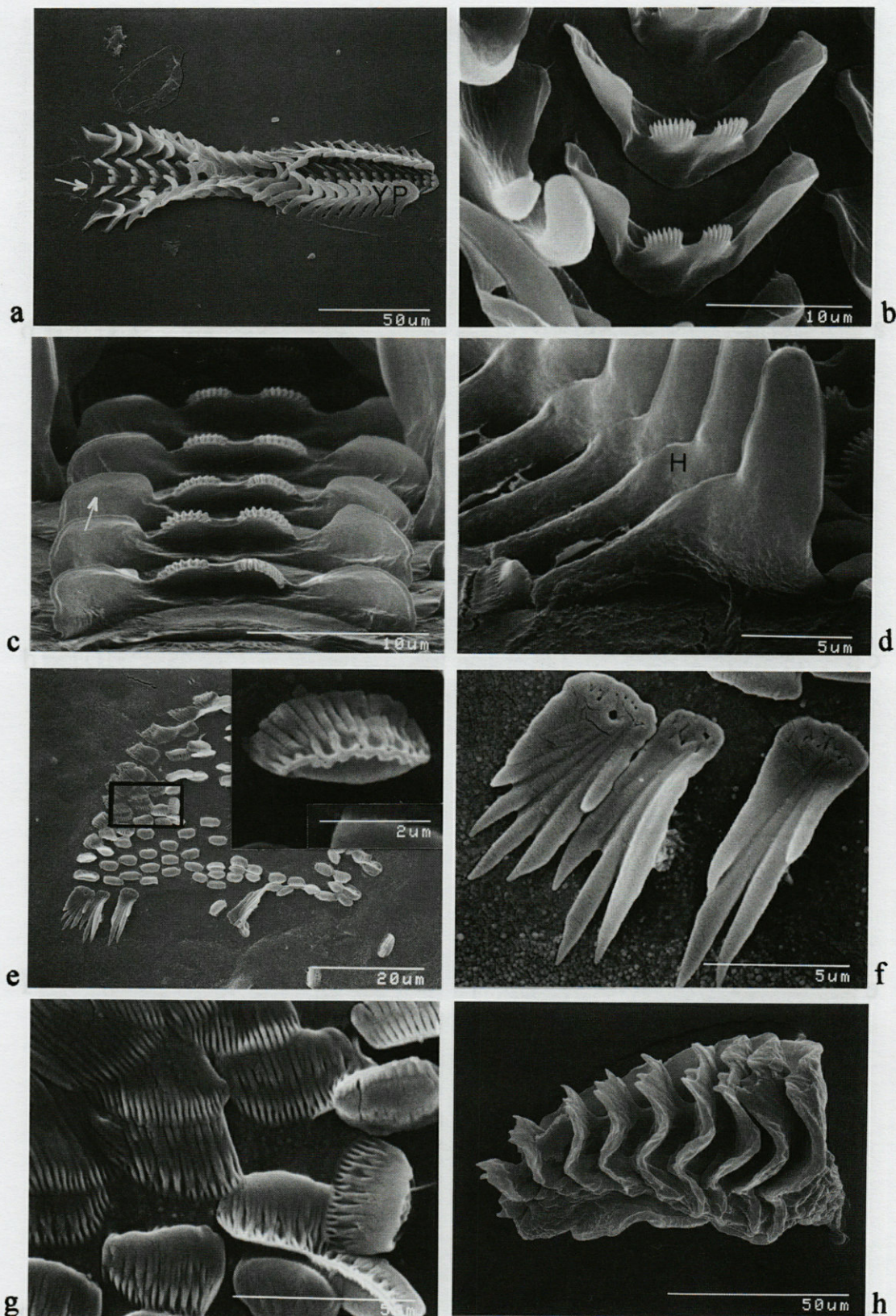


Plate VII. – SEM micrographs. *Runcina hansbechi* Schmekel & Cappellato n. sp.; **a**, total view of adult radula; YP youngest part, arrow: worn down group of teeth; **b**, rachidian teeth; arrow: triangular trough; **c**, rachidian teeth; arrow: erect sides; **d**, lateral teeth; H hump; **e**, jaws from the side of the oesophagus lumen, partially damaged; frame: see 'g'; inset: scale with forked furrows; **f**, plates with pointed prongs; note perforated bases; **g**, scales of 'e' with forked furrows and sharp rim; **h**, triangular gizzard plate.



Anatomy: Triangular jaws with scales (spec. fix. 1.7 mm; Pl. VII e). of very variable shape (Pl. VII e inset, g), with a sharp rim and vertical, often forked grooves (inset) on both sides. On the side facing the gizzard they cover one third of the scale, on the side facing the mouth they do not exceed the horizontal furrow just below the rim. The grooves are forked most on the scales at the margins of either field. 11-12 plates ($10 \times 3 \mu\text{m}$), each with 4-6 very long, pointed, parallel prongs, the largest in the middle of each plate (Pl. VII f). Bases of the plates with minute holes (Pl. VII f).

Radula: $23 \times 1.1.1$ (spec. fix. 1.7 mm, rad. 1.165 μm ; Pl. VII a). Rachidian teeth (19 μm b., sides 12 μm l., 3.5 μm h., cusp 4 μm h.) bilobed (Pl. VII b), the 8-10 relatively short and pointed, diverging denticles of each flatly *Cardium*-shaped cusp forming a slight arc. A deep and broad depression between the pads, no central denticle. Sides very high like wings (Pl. VII c), tilted smoothly inwards. Smooth laterals (Pl. VII d) shaped like a straight duck-neck (18 μm h.); cusps hollow with rounded tips. Bases (18 μm l.) either with or without a hump.

4 triangular gizzard plates (Pl. VII h), 90 μm l., having 9 lamellae with 3 tips each. Basal beam thick, leaving half to two third of the lamellae free. No shell detectable by NaOH maceration or in histological sections.

Etymology: This species is named with loving memories for the late father of D. Cappellato, Dr. Hans Gert Bech.

Discussion. Among the "black" *Runcina* we differentiate between two basic patterns resulting in the impression of "black": 1. Yellowish ground colour covered by black patches (e.g. *R. hansbechi*, Pl. III c). 2. Dark ground colour with black patches like *R. capreensis*, *R. africana* and Gosliner's (1990) *R. adriatica*. There are several species having a yellowish ground colour with black blotches, but compared with *R. hansbechi* there are fundamental differences. For comparison of this new species with *R. banyulensis* n. sp., see discussion there. *R. kressae* has three cross-bands of rounded to oval black patches, an opaque white cross-band behind the eyes and a white notum rear. The body of *R. hansbechi* is covered all over with irregularly shaped black blotches, interspersed with small white spots. The scales of the jaws of *R. hansbechi* show grooves, which often fork (Pl. VII e inset, g), in *R. kressae* they never do so (Pl. VI g). The plates of the jaws of *R. kressae* (Pl. VI f) have shorter and less pointed prongs than those of *R. hansbechi* (Pl. VII f). *R. adriatica* Thompson, 1980 from Rovinj always has rounded, isolated black blotches often lined up in rows and a white cross-band and notum rear (Pl. III e, f), while in *R. hansbechi* the black blotches are variably amoeboid in shape and spread randomly, with white spots distributed evenly among them (Pl. III c). The scales of the jaws in *R.*

adriatica bear unforked vertical grooves only towards the gizzard, but in *R. hansbechi* the grooves are on both sides of the scales and forked (Pl. VII e inset, g). Very characteristic are also the thin, thorn-like, acutely pointed tips of the jaw-plates in *R. hansbechi*. In *R. hansbechi* the rachidians form much higher wings than in *R. adriatica*. *R. capreensis* Mazzearelli, 1894, never rediscovered: three animals have been found by Mazzearelli at 80 m depth at Capri. The body shape is rather similar to that of *R. hansbechi*. Both species have more or less distantly set black blotches, interspersed with white spots, but the ground colour of *R. capreensis* is charcoal black ("bistro") with a yellowish head, whereas the ground colour of *R. hansbechi* is yellowish. On the picture of Mazzearelli (1894; fig. 16) the black patches of *R. capreensis* are smaller, more circular and set more distantly than in *R. hansbechi* where they are variably amoeboid. *R. hansbechi* bears blackish blotches on the yellowish foot sole, Mazzearelli (1894: p. 4) does not mention any black blotches on the yellow foot sole. The rachidians of *R. capreensis*, according to Mazzearelli, resemble those of *Ildica nana* as described by Bergh (1889). *Ildica nana* has rachidians with one smooth and rounded central cusp bearing only one minute denticle on either side. *R. hansbechi* has classical bilobed rachidians with two denticulate cusps, instead.

***Runcina nivale* Schmekel & Cappellato n. sp. (Pl. II e, IV a; part II, Table I)**

Material: Naples, Ischia/Porto (Italy): 2 specs., Oct. 21st, 1967 from sand interstitium, 2 m depth, near the beach (loc. typ.). Due to the sampling method we have seen only the dead animals. Holotype and Paratype at Senckenberg Mus., Frankfurt, N° 322854.

Body shape of fixed holotype (2 mm l., 1 mm w., 0.7 mm h., tail 0.5 mm; Pl. IV) high and droplet-shaped, widest and highest at the notum rear. Front of smooth notum straight, almost no head lobes. Notum rear slightly bilobed (damaged and regenerated?). Foot sole slightly broader than notum; tail very long, broad and rounded. Very large and conspicuous eyes (Pl. IV a), just beneath the epithelium, and close to the anterior border. Anus terminal and median, very large gills to the right side of it, protruding from beneath the notum rear (Pl. IV a), and consisting of three laminae, all subdivided horizontally, up and down. They insert even more tilted than in other species of *Runcina*. **Varieties:** The smaller specimen (paratype, 1.4 mm l.) shows a pointed notum rear and three rounded and undivided gill laminae.

The species is totally whitish transparent, thus the viscera, ganglia and the oesophagus are visible. As a shell probably would be easily detectable due to the transparency of the animals, we conclude that there is none.

Discussion: This species is the only one of the few found in the sand interstitium, which is completely whitish and transparent (perhaps whitish when alive) with large gills and large eyes. Poizat (1978) described another species from the mesopsammnon near Marseille. He found a great number of dark *Runcina* (Pl. XII D) which he identified as *R. coronata* (see discussion *R. coronata*).

Runcina banyulensis Schmekel & Cappellato n. sp. (Pl. II i, IV f, VIII a-h; part II, Table I)

Material: 4 specs: 1 × 0.8 mm l., March 1996; Banyuls, near the Observatoire Arago, from *Posidonia* rhizomes by diving at 5 m depth. 3 × 1.2-1.4 mm l., Sept. 1997; from small rocks outside the Centre Héliomarin, 1.5-2 m depth; Holotype at Senckenberg Mus., Frankfurt, N° 322855.

Holotype (Sept. 26, 1997, Centre Héliomarin, Banyuls, 1.5 m; Pl. IV f) alive 1.2 mm l., 0.5 mm b., 0.3 mm h., tail 0.1 mm. Body shape elongated, scarcely with head lobes. Quick crawler, in movement even more elongated. Widest region of smooth notum behind the middle of the body length. Anterior notal border with a depression, notum rear long and rounded. Alive foot as wide as notum, after fixation foot slightly broader (Pl. IV f). Tail short and rounded. Characteristically large eyes (Pl. II i, IV f) close together, high below the epidermis, and close to the anterior notal border. Anus median and terminal, common genital orifice could not be discerned. One rounded gill lamina, slightly subdivided horizontally, just to the right of the anus.

Ground colour translucent yellowish to light beige, viscera beige to brown. Fine, sharp, isolated black specks (Pl. IV f) on notal surface and furrow, and scarcely scattered on the yellowish foot sole. Notum broadly bordered all around with opaque white spots, interspersed in the head region with some larger red-brown spots, and with red spots further down the body and at the rear. The red and red brown spots bleach quickly after fixation. Behind the eyes a broad opaque white cross-band, another longitudinal band runs along the median line, not reaching the notum rear. Together they form a pure white 'T' without red or brown spots. The posterior border of the cross-band is contoured with large black points. Varieties. Two specs. have a black mark on either side of the foot sole at the insertion of the tail. In the smallest specimen the median white line is absent and the white along the notal margin is less pronounced, but the large eyes are striking, too.

Anatomy: Reverse side of jaws shows triangular fields (90 µm, spec. 0.8 mm l., Pl. VIII f) with papillae (1 µm h.) and scales (max. 6 µm b.). 10 plates (9 × 4.5 µm), mostly with 4 pointed prongs (3 µm l., Pl. VIII g).

Radula formula 22 × 1.1.1 (130 µm l.; spec. 0.8 mm, Pl. VIII a, b). Rachidians (15 µm b., sides 12 µm l., 3 µm h.) bilobed, each flat pad with 8-9

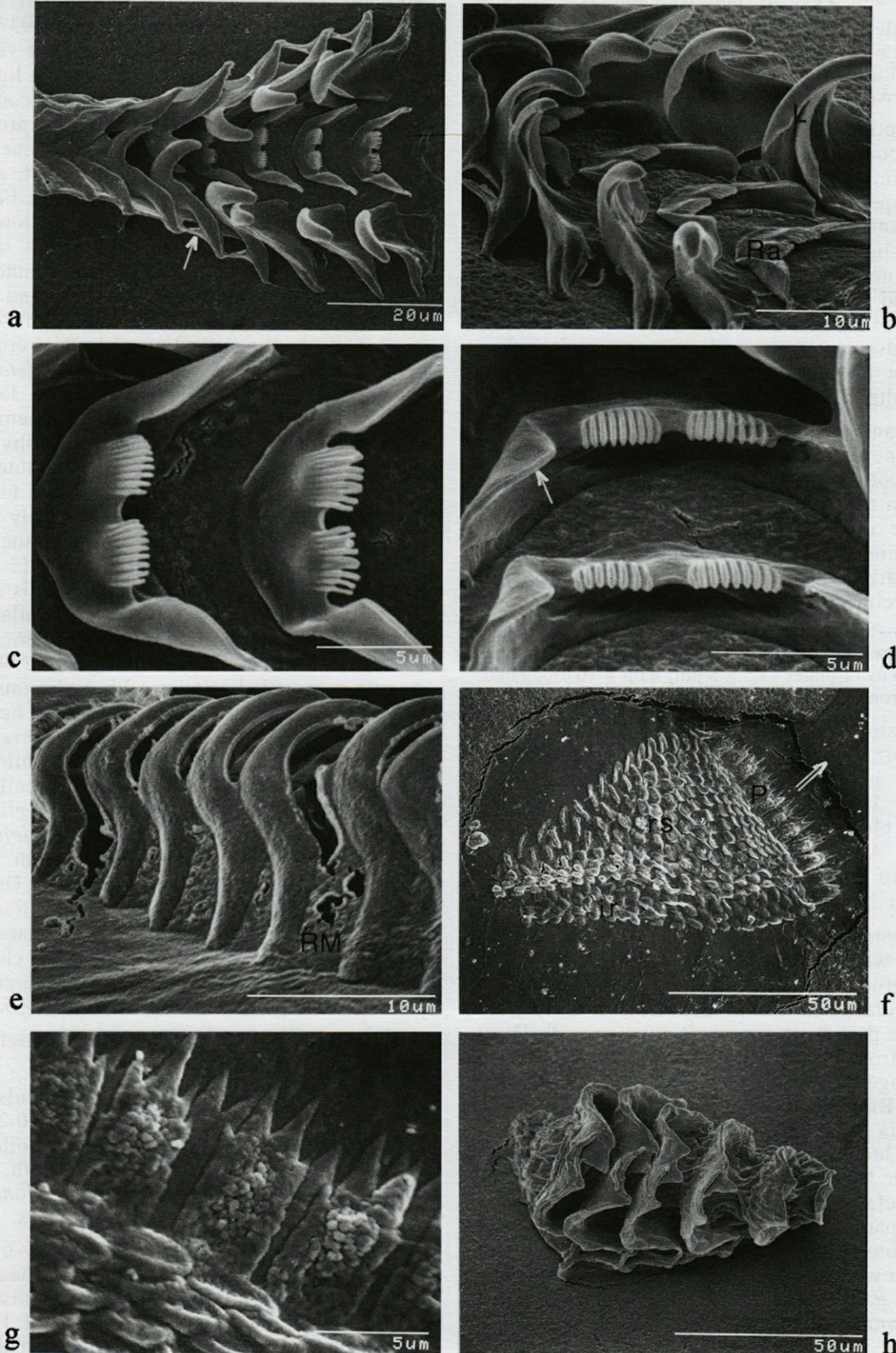
pointed, parallel denticles (2.5 µm l., l. 1.2 µm), more pointed and more diverging in the smaller teeth, and forming a slight arc. Central depression broad (1.2 µm), deep and concave, without central denticle (Pl. VIII c, d). Sides of moderate height, in the highest region tilted angularly inward (Pl. VIII d). Laterals (Pl. VIII b, e) smooth, blunt, swan-necked and without hump (18 µm l. × 15 µm h.). Cusps hollow (Pl. VIII b).

4 boat-shaped gizzard plates (80 µm long) with 1 × 4 and 3 × 6 lamellae (Pl. VIII h) with 2 or 3 tips each. Thick and broad basal beam, leaving half of the lamellae free. N° shell detectable by NaOH maceration or in histological sections.

Discussion. The most characteristic features of *R. banyulensis* are the large eyes, the fine black specks all over, and the red brown to red spots scattered within the opaque white margin of the notum. The black specks scattered on the notum are smaller than in most black spotted species (Pl. IV f).

R. kressae (Pl. III d) is yellowish with three cross lines composed of black spots. But in contrast to *R. kressae* with a narrow white border only laterally, alternating with black patches, *R. banyulensis* has a broad white border all around the notum, mostly interspersed with red or red-brown spots (Pl. II g, i), and no black spots in cross bands. The eyes of *R. banyulensis* are larger and lie higher beneath the epidermis. The arc of the pads in the rachidians of *R. banyulensis* is straighter than in *R. kressae*, their denticles seem to be shorter (Pl. VI c, VIII c). The body shape of *R. hansbechi* is more rounded compared to the slim *R. banyulensis*. In *R. hansbechi* notum and foot are covered with striking, large, amoeboidly shaped black blotches while *R. banyulensis* shows very fine black spots (Pl. III c, IV f). *R. hansbechi* has no opaque white cross-band behind the eyes and no white median line like *R. banyulensis*. While the eyes of *R. hansbechi* are small, they are particularly large in *R. banyulensis*. The radular formula of the two species is similar but the sides of the rachidians are more erect in *R. hansbechi* (Pl. VII c, VIII d). The laterals of *R. banyulensis* are slimmer and more swan-necked, and the gizzard plates have a higher basal beam than those of *R. hansbechi* (Pl. VIII h, VII h). *R. banyulensis* is elongated, in contrast to the squat *R. adriatica* Thompson, 1980 from Rovinj, with pronounced head lobes. The eyes are much larger and higher in *R. banyulensis*. *R. adriatica* has large, rounded, isolated black patches, often arranged in lines, while *R. banyulensis* bears fine sharp black points scattered over the body. Both species have a white cross-band (Pl. II f, j) and mostly a white median line, but only *R. banyulensis* has a broad opaque white notal margin all around. The plates of the jaws of *R. banyulensis* have max. 4 pointed prongs (Pl. VIII g), *R. adriatica* up to 9 blunt prongs (part II, Pl. IV b). The denticles of the rachidians of *R.*

Plate VIII. – SEM micrographs. *Runcina banyulensis* Schmekel & Cappellato n. sp.; **a**, radula; arrow: radular membrane; **b**, radula; Ra rachidian teeth, L lateral teeth; **c**, rachidian teeth; **d**, rachidian teeth with sides tilted inwards (arrow); **e**, lateral teeth; RM radular membrane; **f**, opposite fields of jaws; double arrow: direction to the mouth, rs reverse side, ir imprint of right side through chitinous oesophageal lining, P plates with prongs; **g**, plates with paired prongs, reverse side; **h**, triangular gizzard plate.



banyulensis (Pl. VIII c) do not have an isolated most exterior denticle like those of *R. adriatica* (part II, Pl. IV a).

Runcina avellana Schmekel & Cappellato n. sp. (Pl. II h, V c, IV g, h; part II, Table I)

Material: 3 specs. 1.0, 1.2, 1.5 mm l. Oct. 03, 1995, dredged at night at 5 m depth from *Posidonia* rhizomes, Banyuls, Racou (loc. typ.). Holotype at Senckenberg Mus., Frankfurt, N° 3222856.

Description of the living holotype (Pl. IV c) from Racou, 5m depth: 1.2 mm l., 0.3 mm w., 0.2 mm h., tail 0.3 mm. Very inactive and slow. Body shape very elongated oval and slightly convex, smooth notum almost without head lobes, anteriorly slightly notched, rear short and slightly pointed, not raised. Foot as wide as notum, tail broad and rounded. Small eyes, very deep and close to the front at the inner border of the translucent head sides. Anus and common genital pore could not be detected. One simple rounded gill lamina, slightly to the right of the median line.

Front and sides of the head and tail clear and translucent (Pl. IV c). Notum uniformly chocolate brown, foot sole lighter. Sparse, tiny, opaque white specks on the notum, mainly around the eyes and along the notal margin. No opaque white cross-band behind the eyes. One single round, blackish-brown mark on the centre of the tail (Pl. II h) in all three specimens!

Anatomy: Reverse side of jaws (Pl. V g) of the 1.2 mm spec. set with cup-shaped scales (3.5-10 µm diameter). 10 to 11 plates (3.5 × 8 µm) with 8-10 elongated, pointed prongs (1.8 µm l.).

Surprising for a *Runcina* of 1.2 mm l. is the radula formula $3 \times 1.0.1$ (Pl. V g, h), therefore a probably juvenile radula (see discussion of *R. setoensis* below). Smooth laterals with a high (19 µm), blunt and triangular cusp and a short base (11 µm). After preparation they are clustered together. No gizzard plates and no shell were recovered after NaOH maceration.

Discussion. This is the only chocolate brown *Runcina* with an opaque white sprinkling and a central brown mark on the tail. For comparison with the orange *R. hornae* Schmekel & Cappellato n. sp. see part II (in press). *R. avellana* (Pl. IV c) differs from brownish, juvenile *R. coronata* (Quatrefages, 1844; description in part II, Pl. III), from the Bretagne (compare *R. aurata* from Gibraltar: García *et al.* 1986, and Gosliner, 1990), and *R. ornata* (Quatrefages, 1844), in the elongated body shape (see Cervera *et al.* 1991; p. 200-201, Fig. 2). In Quatrefages' two species it is more oval and convex (part II, Pl. III a). They show distinct head lobes, almost absent in *R. avellana*. Both have at least yellow head sides, which are colourless transparent in *R. avellana* (Pl. IV c). The notum rear of *R. coronata* is cadmium yellow, in *R. ornata* asymmetrically yellowish only on the right side, but

chocolate brown in *R. avellana* (comp. García *et al.* 1986, p. 458-461, Fig 1-4; Cervera *et al.* 1991). In *R. avellana* we found a presumably juvenile radula ($3 \times 1.0.1$) with smooth laterals, so comparison with the adult radulae of the above species with denticulate rachidians and denticulate laterals is inappropriate. *Runcinida elioti* (Baba, 1937), from Oniike, Japan, is dark brown, inclined to yellowish green towards the margin. There are no light head sides like in *R. avellana* and the gill consists of several plumes arranged in a semicircle around the anus, while in *R. avellana* there is one simple rounded lamina slightly to the right. *R. avellana* (Pl. IV c) resembles *R. africana* Pruvot-Fol, 1953 (description in part II, Pl. I f), from Morocco, in the ground colour and the light head sides. *R. avellana* has opaque white spots surrounding the eyes, which are absent in *R. africana*, and a single black spot in the middle of the tail. Additionally *R. avellana* lacks the curved opaque white cross-band behind the eyes of *R. africana*. *Metaruncina setoensis* (Baba, 1954) from Seto, Japan, is blackish with a lighter foot sole, thus resembling *R. avellana*, but its mantle shows an ashy yellow submargin and a sprinkling with minute brown spots. *M. setoensis* has an internal shell, lacking in our species. Baba's species has a greatly reduced radula, not filed up in distinct rows. In the one examined *R. avellana* we found a radula ($3 \times 1.0.1$) arranged in rows. We cannot judge if this radula is juvenile or reduced. It looks very similar to the other juvenile radula found by us (*R. africana*). *R. lenticula* Gofas, Ortea & Rodríguez, 1991, from Angola, a rounded species with a chestnut notum and green flanks and foot, has no light head front and sides and no opaque white like *R. avellana*. It has very characteristic rachidians, not bilobed but with only one central denticle. The juvenile radula of *R. avellana* has no rachidians. *R. avellana* differs from the uniformly brown *R. ferruginea* (description part II, Pl. I a) from Plymouth, Thompson's *R. zavodniki* from Rovinj, and Gosliner's (1991) *R. spec.* from the Azores by its transparent head sides, its white specks and the characteristic single blackish-brown mark on the clear tail. Opaque white and colourless transparent body parts are completely absent in *R. ferruginea*.

Description of a special colour variety of *R. avellana*:

On March 31, 1996 we found at Banyuls a beautiful animal of 1 mm l. × 0.3 mm w. × 0.2 mm h., tail 0.2 mm, from *Posidonia* rhizomes collected by diving near Cap d'Abeille at 8 m depth. We describe it as a colour variety of *R. avellana*, but it may as well be yet another new species.

Body shape very elongated and flatly oval. Anterior notal border straight with small head lobes, posterior end slightly pointed and not raised. Foot as wide as notum, tail short and rounded. Eyes medium sized, close to the buccal mass at the inner

border of the yellow head sides. No anus or common genital orifice could be found. One small, rounded, undivided gill lamina to the right of the median.

Body dark velvet green. Notal margin, foot, gill and tail transparent lemon yellow, wider at anterior notal border and head sides; foot sole with a tinge of brown. A triangular, dark green blotch on either side of the insertion of the tail on the upper foot sole, another small round one in the centre of the tail. Posterior notum end bordered narrowly by dense, small opaque white spots. Animal sparsely covered with tiny white specks and tiny brown specks, somewhat more concentrated along the margins of notum and upper foot, and posterior from the dark marks at the tail.

This dark green animal looks similar to the brown *R. avellana* in body shape and distribution of colour, with some differences: the body shape of *R. avellana* is slightly convex, the green specimen is flatter. *R. avellana* is dark brown with only a single round, blackish-brown mark in the centre of the tail. The single specimen reported here is dark green with translucent yellowish margins and two dark green lateral triangular marks plus a round central one on the tail. This animal externally resembles *R. australis* (Burn, 1963: p. 10-15, Fig. 1-11), a greenish-black species with an ashy-yellow margin, a small inner shell and denticulate laterals. The body of *R. australis* is highly arched, without fine brown or white specks, bearing a small, ashy-yellow triangular patch at the notum rear above the shell. The specimen reported here is elongated oval and flat, its dark green body covered with fine brown and sparse white specks, but without a yellowish patch at the notum rear.

(1) Part of the thesis of the junior author, D. Cappellato.

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GRIFFITHS C.L. and J.A. KING, 1979. Some relationships between size, food availability and energy balance in the Ribbed Mussel *Aulacomya ater*. *Mar Biol* 51 (2): 141-150.

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