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CLETOCAMPTUS RETROGRESSUS (COPEPODA, HARPACTICOIDA) FROM IRRIGATION AND DRAINAGE DITCHES OF THE RHÔNE DELTA (CAMARGUE, FRANCE) A REDESCRIPTION

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CLETOCAMPTUS RETROGRESSUS
COPEPODA HARPACTICOIDA
MORPHOLOGIE
CANAUX
CAMARGUE

RÉSUMÉ. – Des exemplaires de *Cletocamptus retrogressus* Schmankewitsch, 1875 ont été collectionés en Camargue dans des canaux d'irrigation et de drainage (delta du Rhône) de salinité variable. Cette espèce, qui a été trouvée en plusieurs endroits d'Europe, en Afrique et en Asie, restait encore mal connue. Nous la décrivons à nouveau, et tenons compte notamment du dimorphisme sexuel du rostre et des pièces buccales qui sont souvent négligées.

CLETOCAMPTUS RETROGRESSUS
COPEPODA HARPACTICOIDA
MORPHOLOGY
DITCHES
CAMARGUE

ABSTRACT. – Specimens of *Cletocamptus retrogressus* Schmankewitsch, 1875 were collected in the Rhône delta, Camargue, from irrigation and drainage ditches containing water of fluctuating degrees of salinity. Thus far, the species, recorded from many European, African and Asian localities, has been presented only deficiently; in this paper it is redescribed and figured, including the sexualdimorphic rostrum and the mostly neglected mouth parts.

INTRODUCTION

The genus *Cletocamptus* Schmankewitsch, 1875 has a changeable history as to species number, genus synonymy and family affiliation. The diverse species have been classed with genera like *Attheyella*, *Canthocamptus*, *Godetella*, *Marshia*, *Mesochra* or *Regis* and ranked among the Cletodidae or the Canthocamptidae. Actually *Cletocamptus* is integrated in the Canthocamptidae, however, as "incertae sedis" (Por 1986, adopted by Huys *et al*. 1996, Bodin 1997). According to Fleeger (1980) the genus comprises 12 species. 3 new species have been recently added. Gee (1999) described *C. merbokensis* from a mangrove habitat of the Peninsula Malaysia. Mielke (2000) recorded 2 species, *C. axi* and *C. schmidti*, from the Galápagos Archipelago. Some *Cletocamptus* species (*C. deitersi* (Richard, 1897), *C. confluens* (Schmeil, 1894) and *C. retrogressus* Schmankewitsch, 1875) are known to be geographically widespread, morphologically "plastic" and ecologically variable thus implying the existence of morphologically indistinguishable sibling species (Dexter 1995 for *C. deitersi*) or even species conglomerations.

In order to achieve clarity on the systematic position of the respective species at the very least their morphology should be elaborated carefully. The present animals have been collected from the Camargue and attributed to *C. retrogressus*, which has already been recorded from that region (Aguesse & Dussart 1956). The species is now redescribed and illustrated in detail.

MATERIAL AND METHODS

The *Cletocamptus* specimens were collected by Kunert (1991) in different irrigation and drainage ditches of the Rhône delta as co-inhabitants of the plathelminth *Macrostomum romanicum* Mack-Fira, 1968, the real object of her dissertation. The animals were caught by using a hand-net; occasionally the sediment was whirled up beforehand. The concentrate in the hand-net was poured in petri dishes, the copepods were sorted out under a stereo microscope and then fixed in vials in a 4 % formalin solution. 3 ♀♀ and 3♂♂ were dissected and embedded in W 15 medium (Zeiss); the cover glass was sealed with Eukitt and DePeX. Drawings were made with the aid of a camera lucida. The interpretation of body, mouth parts and thoracopods is adopted from Lang (1948; 1965). With respect to the mouth parts, the interpretation of the components according to Huys & Boxshall (1991) is given in parentheses. The material has been deposited in the collections of the Zoological Museum of the University of Göttingen.

DESCRIPTION

Canthocamptidae incertae sedis
Cletocamptus Schmankewitsch, 1875
Cletocamptus retrogressus Schmankewitsch, 1875

Locality: Near to the Plage de Beauduc, Camargue, France. Irrigation and drainage ditches/channels of the Rhône delta (September 1986, leg. T. Kunert; see Kunert 1991); frequent species. 3 ♀♀ and 3 ♂♂ were dissected (reg. nos. I Fra 1-6).

Female

Body length of three dissected females from tip of rostrum to end of furcal rami 0.84-0.94 mm. Distal part of rostrum spinulose, subdistally with a slender setule on each side (Fig. 2A). Dorsal caudal margins of cephalothorax and following 3 somites furnished with weak spinules. Caudal margins of remaining somites as well as ventral caudal margins of abdominal somites set with stronger spinules. Surface of cephalothorax and subcaudal surface of other somites – except of anal and penultimate somites – ornamented with fine setules. Anal somite with a pair of setules in the midst. Genital double-somite subdivided dorsolaterally. Middle part of ventral surface of abdominal somites with rows of spinules, laterally (except anal somite) with irregularly arranged spinules. Distal margin of anal operculum spinulose. Furcal rami about 2.5 times longer than broad. Outer margin proximally with 1 very small seta, at about middle part 2 slender setae stand. Subdistally on dorsal surface 1 seta inserts; it is bipartite at base. Distal margin has 3 setae: inner one naked and short, middle one bulbous on proximal part, fused with slender outer seta; both setae plumose (Fig. 1A, B).

Antennula (Fig. 2A) 6-segmented. Armature of segments: 1 (2 rows of spinules and 1 seta), 2 (9 setae), 3 (6 setae), 4 (2 setae and 1 aesthetasc), 5 (1 seta), 6 (10 setae and 1 aesthetasc).

Antenna (Fig. 3A). Coxa short, furnished with 2 rows of spinules. Anterior margin of allobasis set with slender spinules and obviously with 1 seta only (probably 1 of the proximal spinules in reality represents another seta). Free endopodite segment apically with 1 row of spinules, laterally with some slender and a few stout spinules; anterior margin with 2 spines of different lengths and a small seta. Apical armature represented by 2 slender spines of different lengths, 2 geniculate setae and 1 outer bipinnate seta. Exopodite 1-segmented, slender, bears 3 setae and a few spinules.

Mandible (Fig. 2C). Corpus mandibulae ornamented with rows of slender spinules. Cutting edge with several teeth; 1 unipinnate seta, which is obviously fused to a curved, hyaline structure, inserts laterally. Palpus seems to be slightly variable, consisting of 2 segments, furnished with 1 and 2 setae, respectively.

Maxillula (Fig. 2D, E) with 7 slightly curved, claw-like appendages and 2 plumose spines on distal margin and 1 seta on surface of the praecoxal arthrite. Coxa has 2 setae. Basis, exopodite and endopodite fused; part of basis bears 3 setae apically and 2-3 setae subapically; endopodite represented by 2 or 3 setae, exopodite by 1 seta.

Maxilla (Fig. 2F). Syncoxa ornamented with several rows of spinules; 2 well developed endites distally, each one furnished with 3 elements. Basis (allobasis) has 1 unipinnate claw and 1 seta. Endopodite seemingly weakly 1-segmented, carries 3 slender bare setae.

Maxilliped (Fig. 3B) 3-segmented. Basis (syncoxa) covered with several rows of spinules; 1 short seta arises on distal inner edge. Proximal endopodite segment (basis) as well with several rows of spinules on surface and on inner margin. Distal endopodite segment (endopodite) with 1 slender claw and 1 seta, which inserts at the basal part of the claw.

P1 (Fig. 3C). Coxa subdistally with a row of spinules. Basis furnished with some rows of spinules, and a spine on inner and outer edge, respectively. Exopodite 3-segmented, all segments of about the same length, inner and outer margins spinulose. Outer spines of basal and middle segments slender, middle segment has 1 inner plumose seta. Distal segment bears 2 slender outer spines, 1 bare and 1 plumose seta apically. Endopodite 2-segmented, inner and outer margins of both segments set with slender spinules. Basal segment with 1 plumose seta arising subdistally on inner margin. Distal segment slightly shorter, carries 1 plumose seta subapically and 2 setae apically.

P2-P4 (Fig. 3E, 4A, B). Praecoxae with a row of spinules subdistally on surface. Coxae ornamented with rows of spinules on surface and near outer margin. Bases with spinules at outer lobe and near the insertion point of the endopodites. Outer lobe with a spine (P2) or a slender seta (P3 and P4). Distal middle edge of bases and distal inner margins of proximal endopodal segments of P2 and P3 with a tooth-like extension; in P4 these structures are rather weak. Exopodites 3-segmented; outer margins set with stout spinules, inner margins have slender, hair-like spinules. Proximal and middle segments each with an outer spine, middle segments with 1 inner plumose seta. Distal segments bear 2 bipinnate outer spines, 2 apical plumose setae (except of inner one of P4), and 1 (P2 and P4) or 2 (P3) setae on inner margin. Endopodites 2-segmented. Proximal segments short, distal inner edge produced into a tooth-like extension; inner and outer margins set with slender spinules. Margins of long distal segments as well spinulose, furnished with 4, 5, 2 plumose setae, respectively.

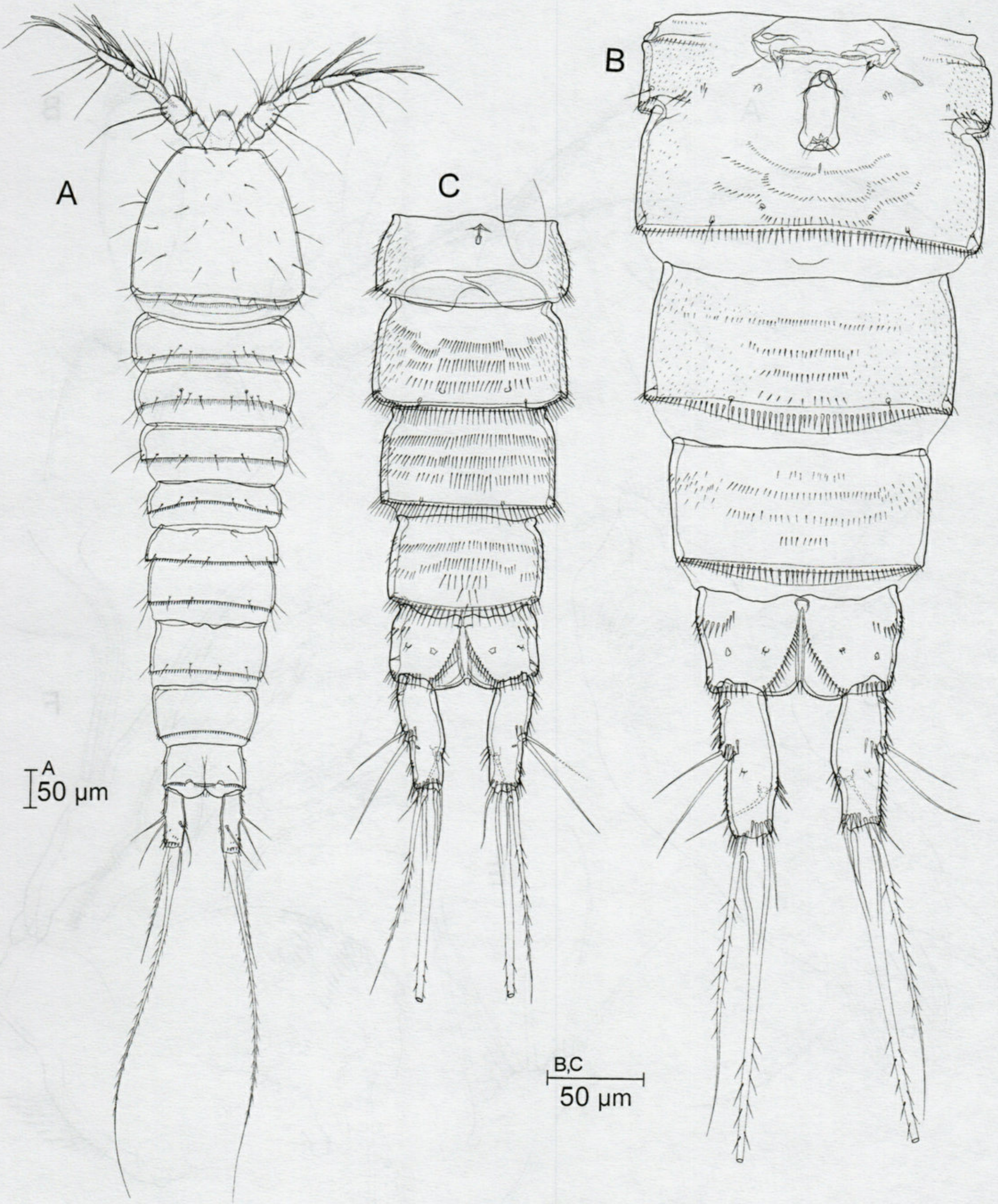

Fig. 1. – *Cletocamptus retrogressus*. A, Habitus dorsal female; B, Abdomen ventral female; C, Abdomen ventral male.

Seta and spine formula:

	Exopodite	Endopodite
P1	(0.1.022)	(1.120)
P2	(0.1.122)	(0.121)
P3	(0.1.222)	(0.221)
P4	(0.1.122)	(0.110)

P5 (Fig. 5A). Baseoendopodite and exopodite fused. Inner part of benp. with 6 pinnate setae of different lengths, outermost but one longest; portion of exp. with 5 setae, innermost but one longest.

Male

Differs from the female in the following respects: Body length of 3 dissected specimens 0.72-0.77 mm. Spinulation of abdominal somites more distinct (Fig. 1C). Length-width ratio of furcal rami somewhat greater. Proximal part of middle terminal seta only slightly bulbous (Fig. 1C). Rostrum more slender (Fig. 2B). Antennula subchirocer. Inner edge of basis P1 tooth-like extended, inner seta slender (Fig. 3D). P2 weakly modified. Basal segment of exopodite P3 (Fig. 5B)

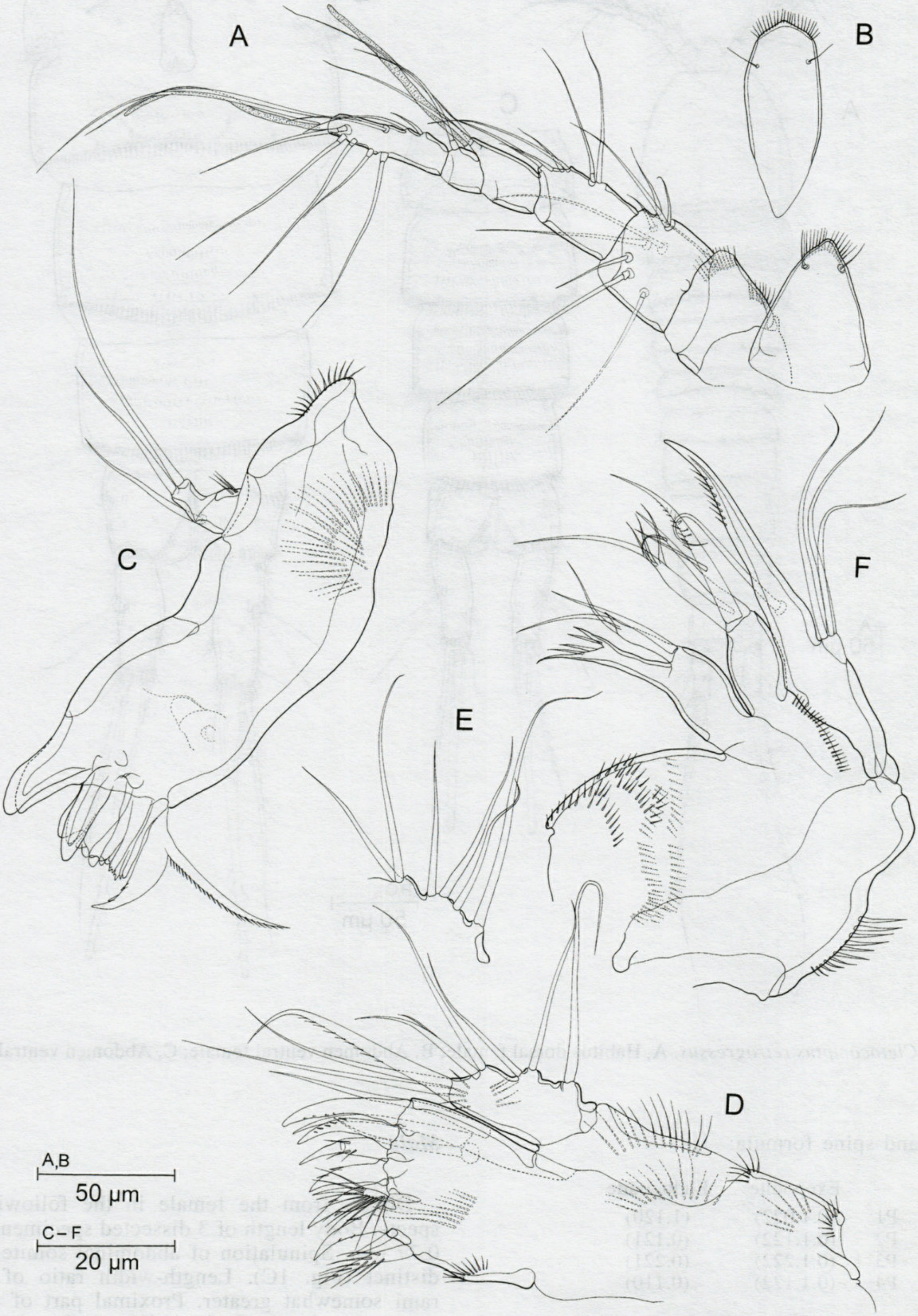

Fig. 2. – *Cletocamptus retrogressus*. A, Rostrum and antennula female; B, Rostrum male; C, Mandible female; D, Maxillula female; E, Outer margin of fused basis, enp. and exp. of other maxillula female; F, Maxilla female.

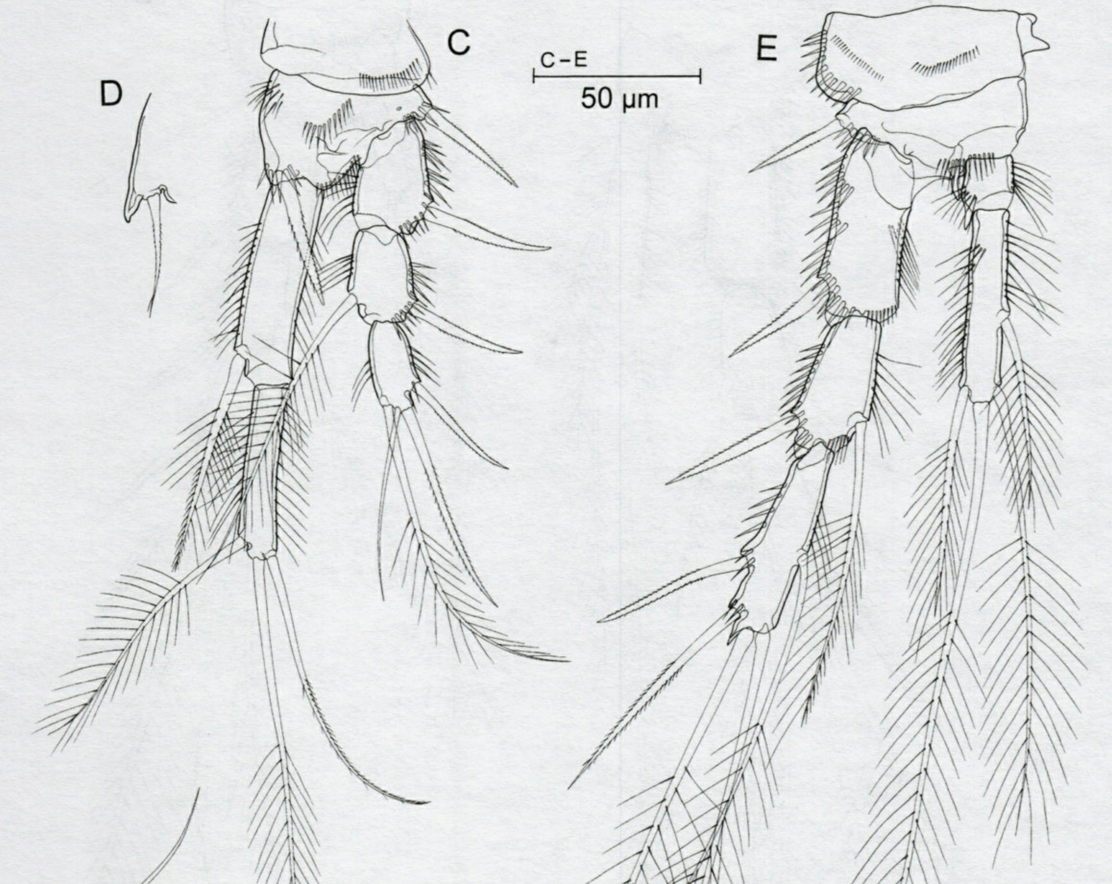

Fig. 3. – *Cletocamptus retrogressus*. A, Antenna female; B, Maxilliped female; C, P1 female; D, Inner margin of basis P1 male; E, P2 female.

Fig. 4. – *Cletocamptus retrogressus*, female. A, P3; B, P4.

enlarged; elements of distal segment shorter, above all apical outer one; endopodite 3-segmented; inner edge of middle segment produced into a spine-like process; distal segment roundish, bears 2 plumose setae. Basal segment of exopodite P4 (Fig. 5C) robust, enlarged; elements of distal segment shorter, above all apical outer one; endopodite corresponds to the one of female, but both setae of distal segment distinctly shorter. Baseoendopodite and exopodite P5 (Fig. 5D) fused; inner part of benp. with 3 (occasionally 4), part of exp. with 4 (occasionally 3) setae. P6 (?) obviously represented by very transparent plates (see Fig. 1C).

DISCUSSION

A multitude of records exists for *C. retrogressus*, often solely in species lists, sometimes completed by ecological or morphological data. Other than the contributions mentioned in

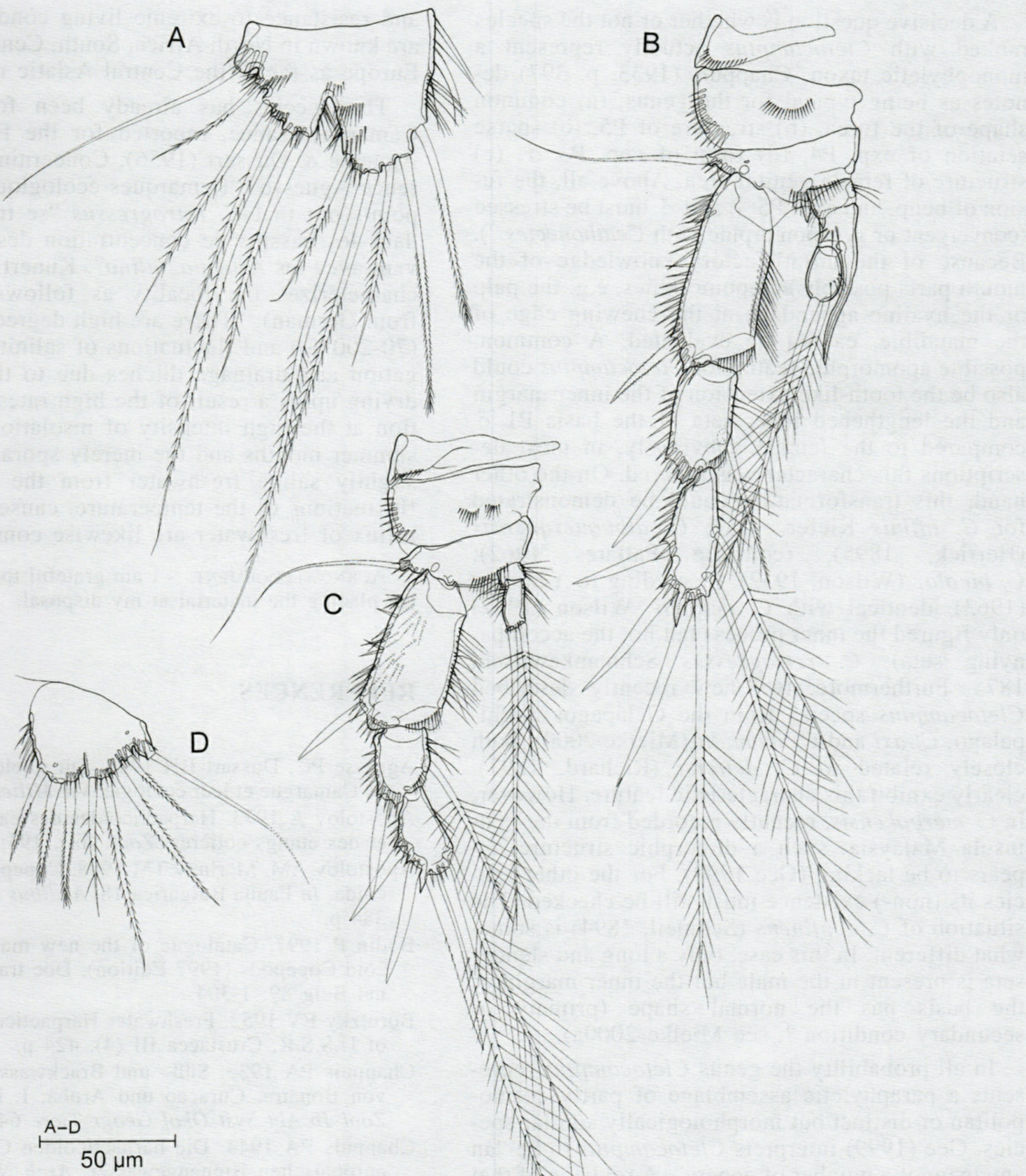

Fig. 5. – *Cletocamptus retrogressus*. A, P5 female; B, P3 male; C, P4 male; D, P5 male.

Lang (1948) several authors give additional figures of the antennula, the antenna, the furcal rami and/or the peraeopods, e.g. Chappuis 1944, Stephanides 1948, Borutzky 1952, Kiefer 1952, Margalef 1953, Aguesse & Dussart 1956, Dussart 1967 (figures adopted by Janetzky *et al.* 1996), Damian-Georgescu 1970, Apostolov 1973, Dumont & Decraemer 1977, Tai & Song 1979, Apostolov & Marinov 1988. In these contributions the mouth parts are usually neglected. Borutzky as well as Damian-Georgescu figure the palp of the mandible, being 2-segmented and furnished with 3 setae. This state corresponds to the one of the present animals. The rudimentary seta at the proximal outer margin of furcal rami is generally overlooked. Furthermore, the different shape of rostrum ♀ and ♂ is not emphasized anywhere. However, Sars (1903) illustrates female and male specimens from the dorsal side whereby the difference can be seen.

A decisive question is whether or not the species ranked with *Cletocamptus* actually represent a monophyletic taxon. Chappuis (1933, p. 397) denotes as being typical for the genus: (a) common shape of the furca, (b) structure of P5, (c) sparse setation of exp. P4, (d) form of enp. P3 ♂, (e) structure of female genital area. Above all, the fusion of benp. and exp. P5 ♀ and ♂ must be stressed (convergent or synapomorphic with *Ceuthonectes* ?). Because of the unsatisfactory knowledge of the mouth parts possible autapomorphies, e.g. the palp or the hyaline appendage at the chewing edge of the mandible, cannot be evaluated. A common, possible apomorphic feature of *Cletocamptus* could also be the tooth-like extension of the inner margin and the lengthened inner seta of the basis P1 ♂ compared to the female. Obviously, in most descriptions this character was ignored. On the other hand, this transformation could be demonstrated for *C. affinis* Kiefer, 1957; *C. albuquerquensis* (Herrick, 1895), (compare Pallares 1962); *C. bicolor* (Wilson, 1932), (according to Yeatman (1963) identical with *C. deitersi*; Wilson (1932) only figured the inner process but not the accompanying seta); *C. retrogressus* Schmankewitsch, 1875. Furthermore, two new recently described *Cletocamptus* species from the Galápagos Archipelago, *C. axi* and *C. schmidti* (Mielke 2000), both closely related to *C. deitersi* (Richard, 1897), clearly exhibit this characteristic feature. However, in *C. merbokensis,* recently recorded from the Peninsula Malaysia, such a dimorphic structure appears to be lacking (Gee 1999). For the other species its (non-) existence must still be checked. The situation of *C. confluens* (Schmeil, 1894) is somewhat different. In this case, only a long and slender seta is present in the male but the inner margin of the basis has the normal shape (primary or secundary condition ?, see Mielke 2000a).

In all probability the genus *Cletocamptus* represents a paraphyletic assemblage of partly cosmopolitan or distinct but morphologically similar species. Gee (1999) interprets *Cletocamptus* to be "an amalgam of a number of genera". A revision of that species complex of unsure systematic relationship is highly desirable, however, the present state of information (mouth parts, sexual dimorphism) for some species is deficient and prevents any serious attempt.

ECOLOGICAL NOTES

Cletocamptus retrogressus is a widely distributed species inhabiting inland waters of very different salinity concentrations such as lakes, lagoons, ponds, ditches – occasionally existing merely temporarily. Locally the species occurs in huge quantities demonstrating its great tolerance and resistance to extreme living conditions. Sites are known in North Africa, South, Central and East Europe as far as the Central Asiatic region.

The species has already been found in the Camargue/France, reported for the first time by Aguesse & Dussart (1956). Concerning the occurrence Aguesse ("Remarques écologiques", p. 506) points out that *C. retrogressus* "se trouve jusque dans les bassins de concentration des salines, vivant avec les *Artemia salina*". Kunert (1991, p. 3) characterizes the locality as follows (translated from German): "There are high degrees of salinity (70-200 ‰) and fluctuations of salinity in the irrigation and drainage ditches due to the transitory drying up as a result of the high rates of evaporation at the high intensity of insolation during the summer months and the merely sporadic influx of slightly saline freshwater from the Rhône. The fluctuations of the temperature, caused by sudden influx of freshwater are likewise considerable".

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ANALYSE D'OUVRAGE/*BOOK REVIEW*

H. KEUPP, 2000. Ammoniten – Paläobiologische Erfolgsspiralen. Jan Thorbecke Verlag (E-mail : info@thorbecke.de), Senefelderstrasse 12, Postfach 4201, D-73745 Ostfildern Allemagne). 165 p., 283 fig., 24 x 28 cm. Couverture : carton rigide et simili tissu. 30.17 Euros.

Pour ce qui est des Céphalopodes en général, le Nautile, seul rescapé vivant d'un groupe très ancien, représente un modèle de recherche apprécié par les paléontologistes et les néontologistes. Par contre, peu de biologistes semblent s'intéresser aux Ammonites, éteintes depuis 65 millions d'années, donc inaccessibles à une recherche biologique. Ce fait est indéniable ; il reste que les Ammonites étaient très probablement parmi les plus proches parents des Coléoidés (Céphalopodes à coquille interne ou absente), aujourd'hui représentés par les Céphalopodes vivants autres que le Nautile. Cette hypothèse de proche parenté émise par des paléontologistes, est importante pour les biologistes qui essaient de comprendre l'évolution des Céphalopodes, et en particulier pour ceux qui s'intéressent aux transformations passées du complexe coquillier.

Voici un livre, rédigé par un paléontologiste, qui fait le point des connaissances acquises sur les Ammonites, présentées dans une optique biologique. Le sous-titre du livre (spirales d'un succès paléobiologique) souligne cette perspective qui enrichit les recherches menées en paléontologie depuis un siècle. Comme le souligne H.-G. Herbig, dans sa préface, les Ammonites allaient de succès en succès pendant 350 millions d'années : après chacune des grandes crises qui avaient balayé la plupart des formes, les quelques survivants avaient les moyens de s'adapter aux conditions changeantes des milieux marins – jusqu'à la fin du Crétacé.

Avant de s'attaquer aux grandes questions de paléobiologie, Keupp rappelle la longue tradition de « l'ammonitologie » ; il rend hommage à U. Lehmann (université de Hambourg) qui avait rendu ce domaine accessible au grand public. Le point de départ de sa propre analyse est la différence morphologique entre la coquille du Nautile et celle des Ammonites, qui soulève le problème des limites d'une comparaison entre le « fossile vivant » qu'est le Nautile et la multitude de « fossiles morts » que représentent les Ammonites. Cet aspect est approfondi dans un chapitre consacré à la position systématique des Céphalopodes vis-à vis des autres Mollusques, et à celle des Ammonites au sein de la classe des Céphalopodes. Un cladogramme synthétique résume les connaissances actuelles, en insistant sur l'éloignement du Nautile par rapport aux Neocephalopoda qui comprennent les Bactrites, les Ammonites, puis les Bélemnites (disparues à la même époque que les Ammonites) et d'autres Coléoidés (Spirule, Seiches, Calmars, Vampyromorphes et Octopodes). Keupp insiste en particulier sur la ressemblance morphologique et structurale de la loge initiale de la coquille chez les Ammonites et la Spirule. Cette ressemblance peut être interprétée comme un caractère synapomorphe, en dépit du sens opposé de l'enroulement de la coquille (exogastrique chez les Ammonites, endogastrique chez la Spirule). En revanche, la correspondance entre le sens de l'enroulement des coquilles de Nautiles et d'Ammonites est probablement une « analogie » (ou convergeance).

A partir des arguments fournis par une analyse comparée des structures et des comportements observés chez les Céphalopodes vivants, Keupp retient trois hypothèses pour une reconstitution bio-morphologique des Ammonites : (1) impossibilité, pour l'animal doté d'une coquille externe, de s'alimenter comme un chasseur actif ; (2) présence d'un mode reproducteur (marqué par une sélection « relativement r ») ainsi que d'appareils branchiaux et brachiaux de type « moderne » (2 branchies, max. 10 bras) ; (3) persistence de caractères plésiomorphes : il de type « chambre obscure », bras dépourvus de structures préhensiles spécialisées, absence d'une poche d'encre.

Un bref rappel traite de la nomenclature et de la taxonomie des Ammonites, en jetant les bases pour le grand chapitre sur la morphologie fonctionnelle et la structure des coquilles, leur ontogénie, les caractéristiques des lignes lobulaires (et leur utilité pour la recherche phylogénétique), le dimorphisme sexuel, le nanisme et le gigantisme, les convergences morphologiques, puis les caractères internes liés à l'ancrage des muscles dans la coquille, la masse buccale avec les mandibules (dont l'inférieure forme un bouclier nomméaptychus) et la radula, les contenus stomacaux et les néphrolithes.

Les interactions synécologiques entre Ammonites et autres organismes (prédation, épœcie, parasitisme) sont abordées avant la synthèse finale sur la phylogenèse des Ammonites et les 350 millions d'années de leur « carrière réussie ».

Une brève description des conditions ayant permis une fossilisation est suivie d'un rappel historique sur le rôle des Ammonites dans les croyances populaires. L'ouvrage se termine par un excellent glossaire et une bibliographie comprenant plus de 500 références.

Ce qui rend ce livre particulièrement attractif, même pour ceux qui éprouvent quelques difficultés à lire l'Allemand, est la tès belle qualité de l'ensemble des illustrations –qualité technique, didactique, esthétique. Le grand format du livre a permis de reproduire des macrophotos (la plupart en couleur) et des clichés de microscopie photonique et électronique sans aucune perte de détail. Ce livre sera apprécié par la communauté scientifique (Sciences de la terre et Sciences du vivant confondues), et il fera date dans la littérature consacrée à une « vulgarisation de haut niveau ».

S. v. Boletzky

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COSMOPOLITANISM AMONG NEMATODES: EXAMPLES FROM EPSILONEMATIDAE

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COSMOPOLITISME
NÉMATODES MARINS
EPSILONEMATIDAE

RÉSUMÉ. – Cosmopolitisme chez les Nématodes: l'exemple des Epsilonematidae. Le cosmopolitisme chez les Epsilonematidae, famille de Nématodes libres marins à distribution mondiale, est illustré par quelques exemples frappants dans quatre des 13 genres reconnus: *Epsilonema, Leptepsilonema, Metepsilonema* et *Perepsilonema*. Les données actuelles sur la répartition de toutes les espèces de la famille des Epsilonematidae sont regroupées en deux tableaux et découlent pour l'essentiel des résultats de nos études taxonomiques de cette famille.

COSMOPOLITANISM
MARINE NEMATODES
EPSILONEMATIDAE

ABSTRACT. – Cosmopolitanism within the Epsilonematidae, a family of free-living marine nematodes with a world-wide distribution, is illustrated by examples from four genera: *Epsilonema, Leptepsilonema, Metepsilonema* and *Perepsilonema*. Tables are provided with distribution data for all species of the family.

INTRODUCTION

Cosmopolitan distributions seem to occur in quite a few meiobenthic taxa. Some species display a rather broad distribution which may be explained by their wide means of dispersal (Gerlach 1977). Transoceanic dispersal of free-living marine nematodes is not rare. However, many cases of taxonomic "identity" are possibly incorrect due to superficial morphological analysis. So data from literature are to be used carefully. A thorough knowledge of the family Epsilonematidae allowed us to observe the distribution of the species in the group, although available data pose some restrictions on information regarding abundance and presence (Gourbault & Decraemer 1996). Two third of the representatives of the family Epsilonematidae are frequent in the marine intertidal interstitial meiofauna and one third in the sublittoral but were until recently unknown from deep sea habitats. A first record of an epsilonematid from bathyal muddy sediments has recently been described (Neira *et al.* submitted). Also, the range of the intraspecific variability is largely unknown.

The aim of this paper is to give a brief account of the raw biogeographical and ecological data gathered during our taxonomical studies of the group, thinking it could be useful for a larger analyse of the cosmopolitanism within meiobenthos.

At present we recognise 13 genera and 89 species of Epsilonematidae.

MATERIALS AND METHODS

Species records are detailed in two tables for non-cosmopolitan (= each species being restricted to a single sea area) and cosmopolitan genera (= including species with a wide distribution over several sea areas) (Tables I, II respectively), together with localities, sea area (based on geographic index of the Aquatic Sciences and Fisheries Abstracts, ASFA database), type of habitat, and grain size of the sediment. All the environmental data are provided in our previous papers or taken from the relevant literature.

Abbreviations used: C: coarse sand, F: fine sand, M: medium sand, VC: very coarse sand; biotic stands for algae: *(Epsilonema byssicola, E. cygnoides, E. longispiculum, E. parvospina)*, red algae (*E. cygnoides*), *Halimeda (Triepsilonema tripapillatum)*, and between byssus threads of *Aulacomya ater* (*E. byssicola*).

RESULTS AND DISCUSSION

Nine of the 39 genera belonging to three subfamilies, have a relatively restricted geographic distribution (Table I). This restricted distribution is

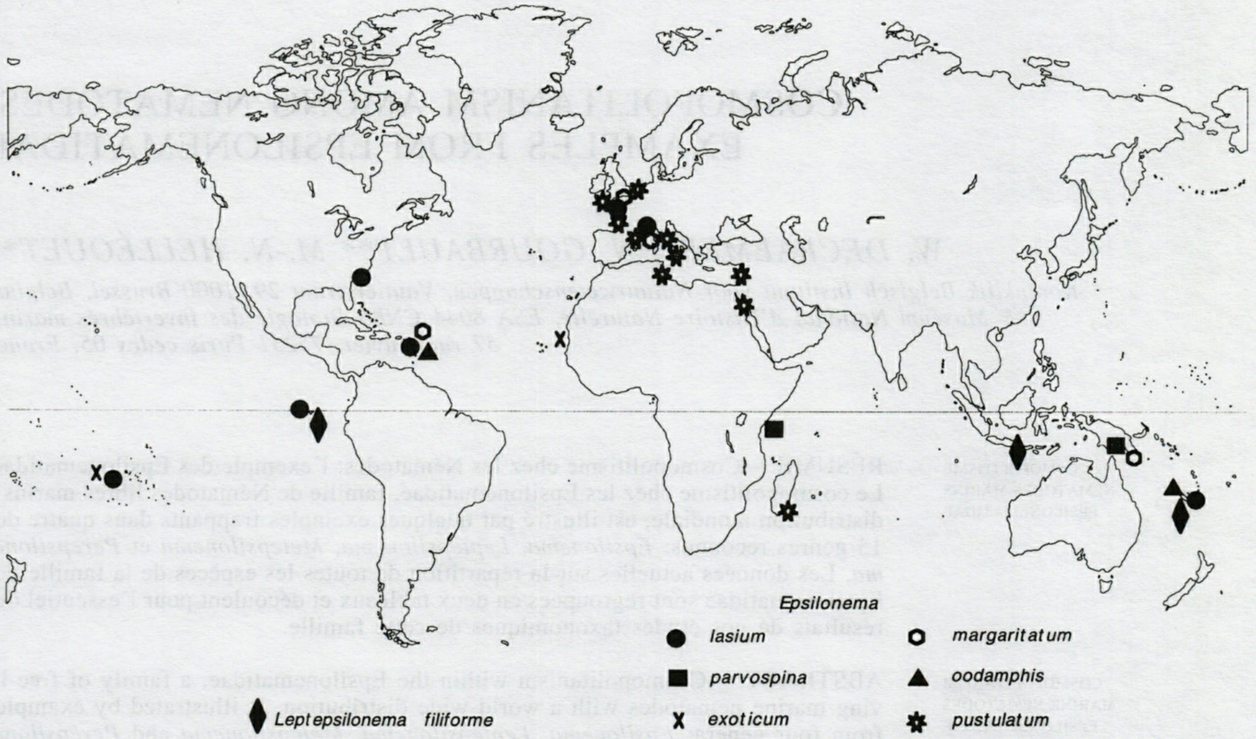

Fig. 1. – Geographic distribution of six cosmopolitan species of the genus *Epsilonema* and of one cosmopolitan species of the genus *Leptepsilonema*.

partly due to five genera being monospecific and known for their type population only. In the other four genera, six of the 17 species are also known from only their type populations and the remaining species are from several localities in the vicinity of their type population. One described but unnamed species is also recorded from a single locality (Jensen 1985). Of these nine genera, it is striking that many representatives are recorded from the South Pacific and the Caribbean Sea; none are from the northern hemisphere above the tropic of Cancer.

The other four genera of the family, *Epsilonema* (23 species, 1 subspecies), *Leptepsilonema* (10 species), *Metepsilonema* (21 species) and *Perepsilonema* (13 species), show a more global distribution which cannot be explained solely by the larger number of species described (Table II). Within these genera, several species show a wide geographic distribution, extended over different geographic regions (= sea areas) as determined by ASFA. Therefore we consider them as cosmopolitan species. Seven out of 23 species of *Epsilonema* (Fig. 1) have been recorded from two or more sea areas (Table II). We did not include *E. byssicola* and *E. serrulatum* because data from ecological papers could not be verified. Among these seven widely distributed species, *E. lasium*, *E. margaritatum* and *E. pustulatum* display a wide geographic distribution in different climate regions. Others are restricted to a similar climate region. For example, *E. exoticum* and *E. parvospina* in the tropical/subtropical girdle. Some species however, exhibit geographical differences in abundance. For example, *E. pustulatum* is common in temperate regions (North Sea, Mediterranean Sea; its occurrence in Madagascar remains to be verified). *Leptepsilonema filiforme* is the only species of this genus with a wide distribution (Fig. 1). Specimens from New Caledonia and Indonesia are larger (340-425 µm and 330-370 µm, respectively, *vs* 250-300 µm) and have longer spicules (41-51 µm and 41-45 µm, respectively, *vs* 25-32 µm, all measured along spicules) than the type specimens described from Galapagos. Attention should be paid to the method used by authors for measuring spicules, since some authors, such as Lorenzen (1973, 1974, 1992) and Clasing (1981, 1984, 1984), measure them by the chord and not along the arc. The nine other species are either true endemic (Myers & de Grave 2000) either restricted to a single geographic area.

Metepsilonema bermudae and *M. callosum* are the most common of the widely distributed taxa of the genus (Fig. 2). For *M. bermudae*, a large variability occurs in spicule length (23-31 µm) within and between populations, the two subventral rows of 5-6 tiny copulatory thorns may be obscured e.g. due to the orientation of mounted specimens and easily overlooked. With *M. callosum*, two morphogroups A and B can be distinguished in

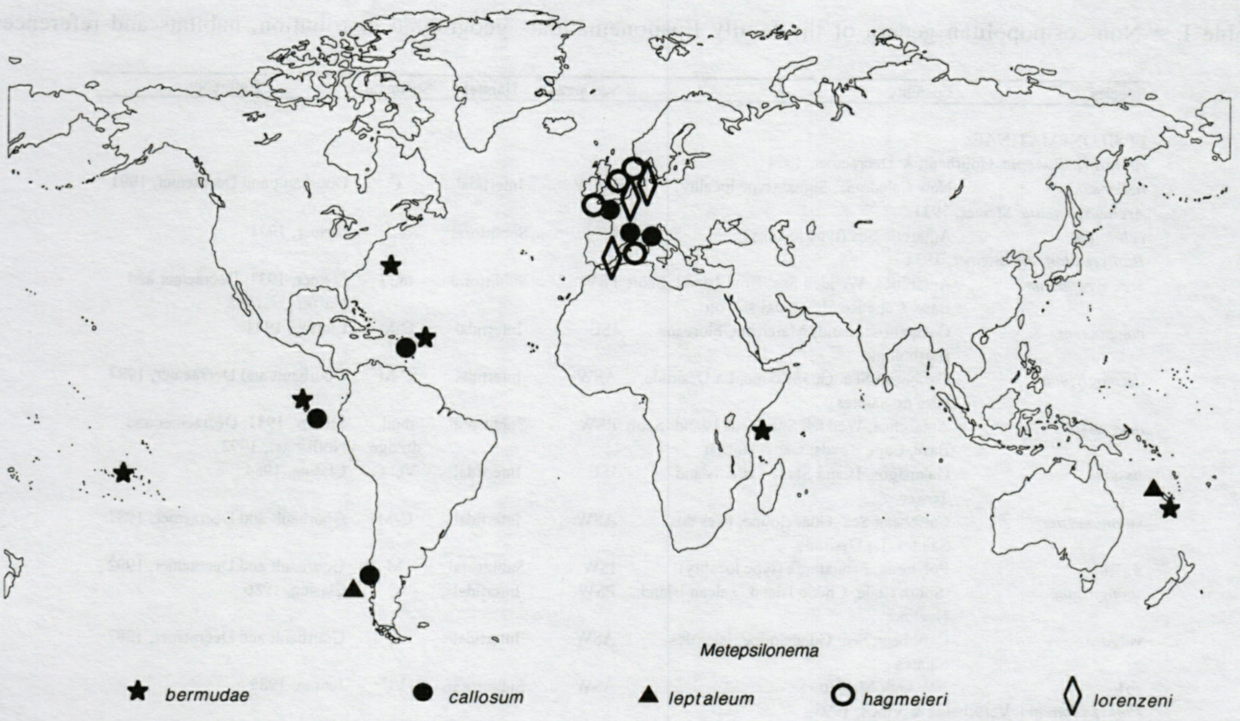

Fig. 2. – Geographic distribution of five cosmopolitan species of the genus *Metepsilonema.*

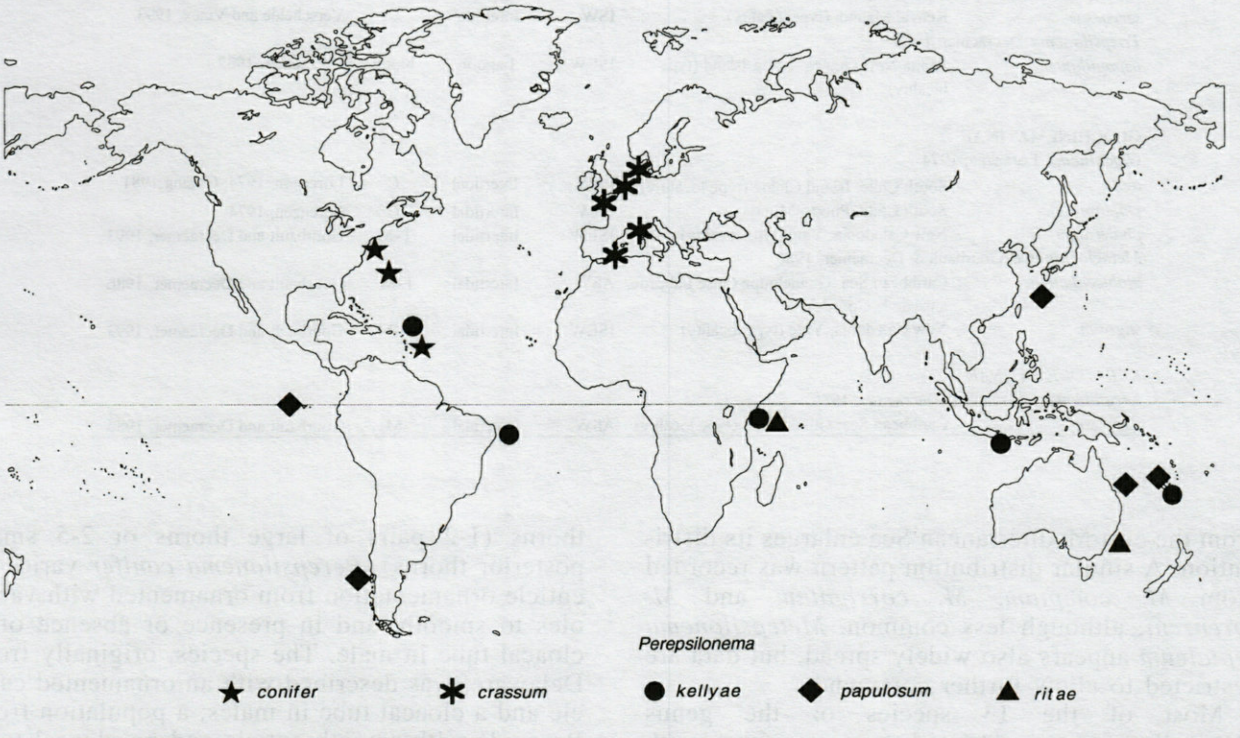

Fig. 3. – Geographic distribution of five cosmopolitan species of the genus *Perepsilonema.*

number of body rings (males: A 99-107 rings *vs* B 110-114; females: A 96-109 *vs* B 111-112), in length of spicules in males (A 33-45 µm *vs* B 48.5-50.5 µm) and in body length (A 205-385 µm *vs* B 365-402 µm); both morphogroups are not geographically separated (Decraemer & Gourbault 2000b). *Metepsilonema hagmeieri* is widely spread in the east North Atlantic region; a new record

Table I. – Non-cosmopolitan genera of the family Epsilonematidae: geographic distribution, habitats and references.

Species	Locallity	Sea areas	Habitat	Sediment	Reference
EPSILONEMATINAE					
Akanthepsilonema Gourbault & Decraemer, 1991					
helleouetae	New Caledonia, Signal (type locality)	ISEW	Intertidal	C	Gourbault and Decraemer, 1991
Archepsilonema Steiner, 1931					
celidotum	Antarctic Sea (type locality)	PSW	Sublittoral		Steiner, 1931
Bathyepsilonema Steiner, 1931					
brachycephalum	Antarctica, Weddell Sea, Ross Island: Scott Base, Cape Royds, Gauss station	PSW	Sublittoral	mud	Steiner, 1931; Decraemer and Noffsinger, 1992
compactum	Galapagos: Islands Marchena, Floreana, Bartholome	ISE	Intertidal	C-M	Clasing, 1984
dermoglyphum	Caribbean Sea: Guadeloupe, La Désirade, Isles de Saintes	ASW	Intertidal	C-M	Gourbault and Decraemer, 1987
drygalskii	Antarctica, Weddell Sea, Ross Island: Scott Base, Cape Royds, Gauss station	PSW	Sublittoral	mud, dredge	Steiner, 1931; Decraemer and Noffsinger, 1992
lissum	Galapagos: Island Santa Cruz, Island Tower	ISE	Intertidal	VC-C	Clasing, 1984
monniotorum	Caribbean Sea: Guadeloupe, Isles des Saintes, La Désirade	ASW	Intertidal	C-M	Gourbault and Decraemer, 1987
salvati	Polynesia, Fangataufa (type locality)	ISW	Sublittoral	M	Gourbault and Decraemer, 1992
spongiosum	South Chile, Chiloé Island, Talcan Island, Huelmo	PSW	Intertidal	C	Clasing, 1986
vulgare	Caribbean Sea: Guadeloupe, Isles des Saintes	ASW	Intertidal	C	Gourbault and Decraemer, 1987
sp1	NW Gulf Mexico	ASW	Sublittoral	VC	Jensen, 1985
Polkepsilonema Verschelde & Vincx, 1993					
firmatum	New Caledonia: Phare Amédée, Isle des Pins, Ilot Signal, Ilot Régnière	ISEW	Intertidal	C-M	Gourbault and Decraemer, 1994a
guirali	Indonesia: Java (type locality)	ISEW	Intertidal	C	Decraemer and Gourbault, 2000a
mombasae	Kenya: Malindi (type locality)	ISW	Intertidal	C	Verschelde and Vincx, 1993
Pternepsilonema Verschelde & Vincx, 1993					
servaesae	Kenya: Malindi (type locality)	ISW	Intertidal	C	Verschelde and Vincx, 1993
Triepsilonema Decraemer, 1982					
tripapillatum	Papua New Guinea: Laing Island (type locality)	ISEW	Lagoon	biotic	Decraemer, 1982
GLOCHINEMATINAE					
Glochinema Lorenzen, 1974					
agile	South Chile: Island Chiloé (type localitly)	PSW	Intertidal	C	Lorenzen, 1974; Clasing,1981
chilense	South Chile: Puerto Montt	PSW	Intertidal	C	Lorenzen, 1974
phaleratum	New Caledonia: Yaté (type locality)	ISEW	Intertidal	F-M	Gourbault and Decraemer, 1993
Metaglochinema Gourbault & Decraemer, 1986					
globicephalum	Caribbean Sea: Guadeloupe (anse Laborde, anse de la Gourde)	ASW	Intertidal	F-M	Gourbault and Decraemer, 1986
stigosum	New Caledonia, Yaté (type locality)	ISEW	Intertidal	F-M	Gourbault and Decraemer, 1993
KERATONEMATINAE					
Keratonema Gourbault & Decraemer, 1986					
singulare	Caribbean Sea: Guadeloupe (type locality)	ASW	Intertidal	M	Gourbault and Decraemer, 1986

from the east Mediterranean Sea enlarges its distribution. A similar distribution pattern was recorded from *M. comptum, M. corrigatum* and *M. lorenzeni*, although less common. *Metepsilonema leptaleum* appears also widely spread, but data are restricted to allow further commend.

Most of the 13 species of the genus *Perepsilonema* are restricted to narrow areas, with the exception of *P. conifer, P. crassum, P. kellyae, P. papulosum* and *P. ritae*. *Perepsilonema kellyae* occurs in sandy sediments of five distant sites (Fig. 3). Morphological variability includes: a) cuticle ornamentation (originally described as smooth, but may be ornamented with vacuoles, partially or over whole body), b) number of copulatory thorns (1-2 pairs of large thorns or 2-5 small posterior thorns). *Perepsilonema conifer* varies in cuticle ornamentation from ornamented with vacuoles to smooth, and in presence or absence of a cloacal tube in male. The species, originally from Delaware, was described with an ornamented cuticle and a cloacal tube in males; a population from Bermuda with smooth cuticle and no cloacal tube in male was subsequently described as subspecies *P. conifer lissum* by Lorenzen 1973. Different populations from Guadeloupe and other Caribbean Islands also present intermediate types of cuticle ornamentation with, for example, only the posterior body region with slightly marked vacuolar ornamentation (best visible on the dorsal side), or

Table II. – Cosmopolitan genera of the family Epsilonematidae: geographic distribution, habitat and references.

Species	Locality	Habitat	Sea areas	Sediment	Reference
EPSILONEMATINAE					
Epsilonema Steiner, 1927					
anulosum	Kenya: Gazi, Malindi	Intertidal	ISW	C	(Verschelde and Vincx, 1992)
***byssicola* ***	South Chile: Island Chiloé	Intertidal	PSW	biotic	Lorenzen, 1973
	Mediterranean Sea: Ischia	Sublittoral	MED	biotic	Novak, 1989
costeriatum	USA, Oregon: Depot Bay (type locality)	Intertidal	ANW		(Murphy, 1963)
cryptamphis	Caribbean Sea: Isles des Saintes (plage de Pompierre),Guadeloupe (Grande Terre, Le Moule), La Désirade (Anse du Souffleur)	Intertidal	ASW	C-M	Decraemer & Gourbault, 1987
***cygnoides* ***	Mediterranean Sea: Salerno, Naples, Island Ischia; Adriatic Sea, Rovinj	Sublittoral	MED	biotic	(Metschnikoff, 1867); Panceri, 1876; Wieser, 1954, 1955, 1956, 1959, 1960; Novak, 1989
	Kiel Bay; Norway (Bergen)	Sublittoral	ANE	biotic	Schulz, 1932; Gerlach, 1958; Schepotieff, 1907-08; Steiner, 1916
	Barents Sea	Sublittoral	PNE		Menzel, 1920
	Westafrica (?)	Sublittoral	ASE		Steiner, 1916
cyrtum	Antarctica: Gauss station, Scott Base, Cape Royds, McMurdo Sound, Weddell Sea	Sublittoral	PSW	mud	Steiner, 1931; Decraemer, 1991
dentatum	South Chile: Island Chiloé (type locality)	Intertidal	PSW	C	Lorenzen, 1973; Clasing, 1986
d. rugatum	New Zealand: South Island, North Island	Intertidal	PSE	C-F	Lorenzen, 1973
docidocricum	Antarctica: Gauss station, Scott Base, Cape Royds, McMurdo Sound	Sublittoral	PSW		(Steiner,1931); Decraemer, 1991
enigmaticum	New Caledonia: Ilot Kouaré (type locality)	Intertidal	ISEW	C	Gourbault and Decraemer, 1994b
espeeli	Kenya: Gazi (type locality)	Intertidal	ISW		Verschelde and Vincx, 1994
exoticum	Polynesia: Moorea Island	Intertidal	ISW	M	Gourbault and Decraemer, 1994
	Senegal, Dakar	Intertidal	ASE	C	new data
fernandinense	Galapagos: Island Fernandina	Intertidal	ISE	VC-C	Clasing, 1984
lasium	South Carolina	Intertidal	ANW	C	Lorenzen, 1973
	Caribbean Sea: Guadeloupe, Iles des Saintes, La Désirade, La Marie-Galante, Martinique	Intertidal	ASW	C-M-F	Decraemer and Gourbault, 1987
	Galapagos: Santa Cruz	Intertidal	ISE	VC-C	Clasing, 1984
	Polynesia: Moorea Island, Fangataufa Atoll	Intertidal; Lagoon	ISW	M; F	Gourbault and Decraemer, 1992; Gourbault and Renaud-Mornant, 1990
	New Caledonia: Thio, Kouaoua, Maa, Yaté	Intertidal	ISEW	M-F	new data
	Mediterranean Sea: Marseille	Sublittoral	MED		new data
	Channel: Sables-d'Or-les-Pins	Salt marsh	ANE		Lorenzen, 1992
longispiculum	Papua New Guinea: Laing Island	Intertidal/Lagoon	ISEW	biotic	Decraemer, 1982
mangrovense	Galapagos: Santa Cruz	Intertidal	ISE	VC-C	Clasing, 1984
	Caribbean Sea: Guadeloupe, Le Moule, Iles des Saintes, La Marie Galante, Martinique, Antigua, Porto Rica, Jamaica	Intertidal/Lagoon	ASW	C-M-F	Decraemer and Gourbault, 1987
margaritatum	Caribbean Sea: Guadeloupe, Jamaica	Intertidal/Lagoon	ASW	M	Decraemer and Gourbault, 1987
	Papua New Guinea, Laing Island	Intertidal/Lagoon	ISEW	C	new data
	Channel	Sublittoral	ANE	C	new data
	Mediterranean Sea: Marseille	Sublittoral	MED	C	new data
meunierorum	Caribbean Sea: Isles des Saintes, La Désirade, Guadeloupe	Intertidal	ASW	C-M-F	Decraemer and Gourbault, 1987
oodamphis	Caribbean Sea: Martinique	Intertidal	ASW	M	Decraemer and Gourbault, 1987
	New Caledonia: Kouaoua	Intertidal	ISEW		new data
paralasium	Caribbean Sea: Guadeloupe (le Moule, anse Laborde)	Intertidal/Lagoon	ASW	C	Decraemer and Gourbault, 1987
parvospina	Papoua New Guinea: Laing Island	Intertidal/Lagoon	ISEW	biotic	Decraemer, 1982
	Kenya, Malindi	Intertidal	ISW	C	Verschelde and Vincx, 1994
pustulatum *	Mediterranean Sea: Cannes, Canet, Naples, Tunis, Beirut	Intertidal/Sublittoral	MED		(Gerlach, 1952), 1953-1955; Ax, 1969; Lorenzen, 1973
	Mediterranaean Sea: Marseille, Corsica, Sicily, Recco	Intertidal/Sublittoral	MED	C	new data

with vacuoles present only in the anterior body region. Consequently, the subspecies allocation was considered inappropriate (Gourbault & Decraemer 1988). Males from the Antilles lack a cloacal tube; other cosmopolites do not exhibit variability in any of the features considered diagnostic between populations.

Table II. – *(continued)*

Species	Locality	Habitat	Sea areas	Sediment	Reference
	Northeast Atlantic (Arcachon), Channel (Exe, Scilly Island), North Sea	Intertidal/Sublittoral	ANE	M-C	Renaud-D.,1963; Lorenzen, 1973; Warwick, 1970;Willems *et al.*, 1982; Vincx, 1986
	Red Sea; Madagascar	Sublittoral	ISW		Gerlach, 1958,1964
serrulatum *	South Chile: Island Chiloé	Intertidal	PSW	C	Lorenzen, 1973, Clasing, 1986
	North Sea	Sublittoral	ANE		Willems *et al.*, 1982; Vincx, 1986
spinulosum	Channel: Sables-d'Or-les-Pins	Salt marsh	ANE		(Lorenzen, 1992)
Leptepsilonema Clasing, 1983					
antonioi	Mediterranean Sea: Marseille, Livorno	Sublittoral	MED	C	Decraemer and Gourbault, 2000a
dauvini	Channel (type locality)	Sublittoral	ANE	VC	Decraemer and Gourbault, 2000a
exile	North Chile: Iquique (type locality)	Intertidal	PSW		Clasing, 1983; Gourbault and Decraemer, 1987
filiforme	Galapagos: Island Marchena,Island Bartholome, Island Tower	Intertidal	ISE	VC-C	Clasing, 1984
	New Caledonia: Ilot Signal, Ilot La Régnière	Intertidal	ISEW	C-M	Gourbault and Decraemer, 1995
	Indonesia: Djakarta	Intertidal	ISEW	C	new data
horridum	Japan: Riukin Island (type locality)	Sublittoral	INW	C	Decraemer and Gourbault, 2000a
macrum	South Chile, Puerto Montt (type locality)	Intertidal	PSW	C	Clasing, 1983
parafiliforme	Caribbean Sea: Guadeloupe (type locality)	Intertidal	ASW	F	Gourbault and Decraemer, 1987
procerum	Colombia: Island San Andrés	Intertidal	ASW	C	Clasing, 1983
	Caribbean Sea: Guadeloupe	Intertidal	ASW	C	Gourbault and Decraemer, 1987
richardi	Kenya: Malindi (type locality)	Intertidal	ISW	C	Verschelde and Vincx, 1992
santii	Mediterranean sea: Alicante (type locality)	Sublittoral	MED	VC	Gourbault and Decraemer, 1995
Metepsilonema Steiner, 1927					
acanthum	Galapagos: Marchena	Intertidal	ISE	C	Clasing, 1984
amphidoxum	Channel	Sublittoral	ANE	C-M	Decraemer and Gourbault, 2000b
bermudae	Bermuda	Intertidal	ANW		Lorenzen, 1973
	Caribbean Sea: Guadeloupe, La Désirade, Les Saintes, La Marie Galante	Intertidal	ASW	C-M	Decraemer and Gourbault, 1990a
	Galapagos islands: Bartholome, Santa Cruz, Fernandino, Marchena,Tower, James, Hood	Intertidal	ISE	VC-C-M	Clasing, 1984
	Polynesia, Moorea	Intertidal	ISE	C	Gourbault and Decraemer, 1992
	New Caledonia: Amédée, Touho, Vaata	Intertidal	ISEW	C-M-F	new data
	Kenya: Gasi, Mombasa	Intertidal	ISW	C	Verschelde and Vincx, 1994
callosum	South Chile: Puerto Montt	Intertidal	PSW		Lorenzen, 1973
	Galapagos Islands: Santa Cruz, Marchena, Floreana, Tower	Intertidal	ISE	C-M-F	Clasing 1984
	Caribbean Sea: Guadeloupe, La Désirade, Isles des Saintes	Intertidal	ASW	VC-C-M mud	Decraemer and Gourbault, 1990b
	Channel	Sublittoral	ANE	C	Decraemer and Gourbault, 2000b
	Mediterranean Sea: Marseille, Corse	Sublittoral; Intertidal	MED		Decraemer and Gourbault, 2000b
chilotum	South Chile: Island Chiloé, Island Quinchao	Intertidal	PSW	C	Clasing, 1986
clasingae	Caribbean Sea: Guadeloupe, La Désirade	Intertidal	ASW	M-F	Decraemer and Gourbault, 1990a
	Columbia	Intertidal	ISE	M-F	Clasing, 1981
comptum	Channel	Sublittoral	ANE	C	Decraemer and Gourbault, 2000b
	Mediterranean Sea: Marseille	Sublittoral	MED	C	Decraemer and Gourbault, 2000b
corrugatum	Channel	Sublittoral	ANE	C	Decraemer and Gourbault, 2000b
	Mediterranean Sea: Marseille, Livorno	Sublittoral	MED	C	Decraemer and Gourbault, 2000b

**Most data from ecological papers could not be verified.*

CONCLUSIONS

Epsilonematids, unknown from deep-sea habitats (except for a new discovery), are frequent in the marine intertidal interstitial meiofauna. They occur in coarse sand mostly, but can also be found in other types of habitat. The distribution of cosmopolitan species is not necessarily linked to climate regions. The percentage of cosmopolitan widely distributed species is highest in *Perepsilonema* (40 %).

From Tables I and II appears that 65 species are known from a single location, 13 species from two locations, 4 species from three locations, 2 species from four locations, 3 species from five locations,

Table II. – *(continued)*

Species	Locality	Habitat	Sea areas	Sediment	Reference
Metepsilonema Steiner, 1927					
cuspidatum	USA: Delaware Bay (type locality)	Intertidal	ANW	C	Lorenzen, 1973
glutinosum	Caribbean Sea: Guadeloupe (anse à la Gourde, Pointe des Cahateau, Porte d'Enfer, Anse Laborde)	Intertidal	ASW	C	Decraemer and Gourbault, 1990a
***hagmeieri* ***	North Sea: Helgoland, Sylt	Sublittoral	ANE	C	(Stauffer, 1925); Steiner, 1927; Gerlach, 1952-1954
syn. emersum	North Sea: Sylt	Sublittoral	ANE		Westheide, 1967; Smith, 1969
	North Sea: Helgoland, Sylt	Intertidal	ANE		Lorenzen, 1973; Blome, 1982, 1983
	North Sea: Belgian coast	Sublittoral	ANE	C-M	Willems *et al*.,1982;Vincx, 1986
	Norway (Tromso)	Intertidal	ANE		Schmidt (1972)
	Channel	Sublittoral	ANE	C-M	Clasing, 1981; Decraemer and Gourbault, 1998
	Channel: Scilly Island	Intertidal	ANE		new data
	Arcachon (Atlantic)	Intertidal	ANE	M	Renaud-Debyser, 1963
	Mediterranean Sea: Marseille	Sublittoral	MED		new data
hardyi	Caribbean Sea: Guadeloupe, La Désirade	Intertidal	ASW	C-M	Decraemer and Gourbault, 1990b
iuvenisspinosum	Kenya: Mombasa (type locality)	Intertidal	ISW		Verschelde and Vincx, 1994
laterale	New Zealand: South Island	Intertidal	PSE	F	Lorenzen, 1973
laureli	Caribbean Sea: Guadeloupe, Iles des Saintes	Intertidal	ASW	C-F	Decraemer and Gourbault, 1990b
leptaleum	South Chile: Island Chiloé	Intertidal	PSW	C	Lorenzen, 1973; Clasing 1986
	New Caledonia: Wegon, Vaa	Intertidal	ISEW	M	new data
limbatum	New Zealand: South Island	Intertidal	PSE	C-M	Lorenzen, 1973
lorenzeni	Mediterranean Sea: Alicante (type locality)	Sublittoral	MED	C	Decraemer and Gourbault, 1998
syn. M. hagmeieri sensu Lorenzen, 1973	North Sea: Helgoland; North Sea: Sylt, Channel	Intertidal intertidal sublittoral	ANE	C-M	Lorenzen 1973 Clasing 1981
magdae	Caribbean Sea: Guadeloupe, La Désirade, Iles des Saintes	Intertidal	ASW	C-M	Decraemer and Gourbault, 1990a
striatulum	Caribbean Sea: Guadeloupe, Iles des Saintes, La Désirade	Intertidal	ASW	C-M	Decraemer and Gourbault, 1990a
volutum	Channel	Sublittoral	ANE	VC-C	Decraemer and Gourbault, 2000b
sp,	Channel	Sublittoral	ANE	VC	Decraemer and Gourbault, 2000b
Perepsilonema Lorenzen, 1973					
bahiae	Brasil: Salvador (type locality)	Intertidal	ASW		(Gerlach, 1957)
conifer	USA: Delaware Bay	Intertidal	ANW	C-M	Lorenzen, 1973
	Bermuda	Intertidal	ASW		Lorenzen, 1973
	Caribbean Sea: Guadeloupe, La Désirade, Iles des Saintes, La Marie-Galante, Martinique	Intertidal/Lagoon	ASW	M-F	Gourbault and Decraemer, 1988
coomansi	Mediterranean Sea: Calvi	Sublittoral	MED	VC	Vanreusel and Vincx, 1986
corsicum	Mediterranean Sea: Calvi, Marseille	Sublittoral	MED	M-C	Vanreusel and Vincx, 1986; new data
crassum	North Sea: Helgoland; Belgian Coast	Sublittoral	ANE	C; M	Lorenzen, 1973; Jensen, 1976
	Channel	Sublittoral	ANE	C	Clasing, 1981; new data
	Mediterranean Sea: Calvi; Alicante	Sublittoral	MED	C	Vanreusel and Vincx, 1986; new data
kellyae	Caribbean Sea: Guadeloupe, La Désirade	Intertidal	ASW	M-F	Gourbault and Decraemer, 1988
	New Caledonia: Thio, Amédée	Intertidal	ISEW	M-F	new data
	Kenya: Gazi	Intertidal	ISW		Verschelde and Vincx, 1994
	Indonesia: Djakarta, Bali	Intertidal	ISEW	C	new data
	Brasil: Recife	Sublittoral	ASW	C	new data
longispiculosum	Mediterranean Sea: Calvi; Marseille	Sublittoral	MED	VC	Vanreusel and Vincx, 1986; new data
mediterraneum	Mediterranean Sea: Calvi; Porte Vecchio	Sublittoral; Intertidal	MED	M	Vanreusel and Vincx, 1986; new data
moineaui	Polynesia: Moorea	Intertidal	ISE	C	Gourbault and Decraemer, 1992
papulosum	South Chile: Puerto Montt	Intertidal	PSW	C	Lorenzen, 1973
	Galapagos: Islands Fernandina, Floreana, James, Pinta, Santa Cruz	Intertidal	ISE	VC-M	Clasing, 1984
	New Caledonia: Kouaré	Intertidal	ISEW	M-F	new data
	Australia: One Tree I.	Intertidal	ISEW		new data
	Japan: Miyakojima, Bora Bay	Lagoon	INW	M-F	new data
ritae	Kenya: Gazi	Intertidal	ISW		Verschelde and Vincx, 1994
	Australia: Moruya	Intertidal			new data
trauci	South Chile: Island Chiloé	Intertidal	PSW	C	Lorenzen, 1973; Clasing, 1981
tubuligerum	Caribbean Sea: Guadeloupe, La Désirade, Iles des Saintes, Martinique	Intertidal	ASW	C-M	Gourbault and Decraemer, 1988

** Most data from ecological papers could not be verified.*

a single species from six locations and 1 species from seven locations. This distribution differs significantly from a zero-truncated Poisson distribution where all species have a completely cosmopolitan distribution. Solving the equation for this zero– truncated Poisson distribution gives a mean value of 1.11 opposed to 1.56 calculated from the above data. The distribution of the zero-truncated Poisson distribution is much more even than the observed data, which has too many ones and too few higher numbers. If we consider the number of geographic areas per species, 66 species are known from a single area, 15 species from two areas, two species from three areas, four species from four areas, one species from five and a single species from seven of the total 14 geographic areas differentiated by the ASFA. So we can quite categorically say that some species have a world-wide distribution whereas others are more restricted.

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RÔLE DES FACTEURS ABIOTIQUES SUR LE TAUX DE CROISSANCE D'*ULVA RIGIDA* DANS DEUX SITES MÉRIDIONAUX

Abiotic factors impact on Ulva rigida *relative growth rate in two Southern sites*

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ULVA RIGIDA
TAUX DE CROISSANCE
ETANGS DU SUD
VARIABLES ENVIRONNEMENTALES
A.C.P.

RÉSUMÉ. – Deux stations à *Ulva rigida* C. Agarth, l'une dans l'étang de Thau (Sète, France), l'autre dans la lagune de Venise (Lido, Italie), sont suivies durant une année sur le plan des facteurs environnementaux : salinité, température, lumière incidente, azote (DIN) et phosphore dissous (DRP), et sur le plan des facteurs biotiques : biomasse *in situ* et taux de croissance (RGR) des Ulves en cages. L'A.C.P. relative aux variables environnementales met en avant la liaison « salinité-température de l'eau » à Thau, et la liaison « salinité-lumière incidente » au Lido de Venise. Contrairement au shéma classique, la courbe du RGR annuel, prioritairement sous la dépendance de l'évolution thermique, est bimodale (pics printannier et automnal). Les A.C.P. des facteurs biotiques et abiotiques ajoutent la certitude qu'à Venise le taux faible de phosphates limite le pic printannier du RGR, tandis qu'à Thau le pic automnal est fortement réduit par une lumière incidente faible (conséquence des processus de dégradation estivaux). Les valeurs relativement basses du RGR (< 10 %d^{-1}) sont discutées.

ULVA RIGIDA
RELATIVE GROWTH RATE
SOUTHERN LAGOONS
ENVIRONMENTAL FACTORS
P.C.A.

ABSTRACT. – Environmental factors: water salinity, temperature, incident light, dissolved inorganic nitrogen (DIN), dissolved reactive phosphorus (DRP), and biotic factors: *Ulva rigida* biomass in field and relative growth rates (RGR) in cages of the two Mediterranean stations (Chanel of the Thau lagoon, France and Venice Lido, Italy) were compared. Principal Componant Analysis of environmental variables shows the linkage « salinity-temperature » in the eutrophicated Thau lagoon, and the linkage « salinity-incident light » in Venice Lido. Due to the water temperature the annual *Ulva rigida* RGR curve is bimodal (spring and autumn peaks) in contrast to the unimodal classical sheme. The PCA of biological and environmental variables underlines the DRP as the most limiting factor in spring at Venice Lido station and the incident light as a strigent limiting factor for autumn growth in the Thau lagoon.

INTRODUCTION

La Chlorophycée *Ulva rigida* C. Agardh, espèce opportuniste se développant dans des milieux eutrophisés est sujette à des blooms importants, pouvant provoquer des marées vertes (Piriou *et al.* 1989, Geertz-Hansen & Sand-Jensen 1992, Dion & le Bozec 1996, Fletcher 1996, Romero *et al.* 1996) et peut contribuer à provoquer des crises distrophiques au moment de sa dégradation (Zaouali 1977, Sfriso *et al.* 1987, De Casabianca 1989, Pugnetti *et al.* 1992, Viaroli *et al.* 1992, 1993).

Elle est particulièrement développée dans les deux lagunes méditerranéennes de Thau et de Venise où son développement a été étudié (Sfriso 1995, Sfriso & Marcomini 1997, 1999, De Casabianca & Posada 1998). Les concentrations en sels nutritifs de ces lagunes sont supérieures à celles de la mer (Tournier *et al.* 1983) et à celles des autres étangs méditerranéens (De Casabianca *et al.* 1997a). La comparaison des deux lagunes (Tabl. I) montre un niveau d'eutrophisation plus important à Thau affecté par une activité conchylicole dominante (De Casabianca 1977, Tournier *et al.* 1983, De Casabianca 1996), tandis qu'à Venise, les acti-

Tabl. I. - Caractéristiques des variables environnementales dans les lagunes de Thau et Venise. Moyennes annuelles et extrêmes. D.I.N. (Azote Inorganique Dissous) ; D.R.P. (Phosphore Réactif Dissous) (Sfriso *et al.* 1989 et 1995 pour Venise ; de Casabianca *et al.* 1997a pour Thau).

Main characteristics of Thau and Venice lagoons. Annual means and/or ranges. D.I.N. (Dissolved Inorganic Nitrogen); D.R.P. (Dissolved Reactif Phosphorus) (Sfriso et al. 1989, 1995 for Venice, de Casabianca et al. 1997 a for Thau).

Lagune		**Thau**	**Venise**
Latitude / Longitude		43°24 N et 3°35 E	45°22 N et 12°6 E
Profondeur (m)	Moyennes	~ 3,8	~ 1
	Extrêmes	12	5
Variations niveau (m)		+/- 0.15	+/- 1
Surface (km^2)		75	549
Renouvellement(Volume total)		1,5 mois	20 heures
Salinité (PSU)	Moyennes	36	28
	Extrêmes	29-42	25-33
Température (°C)	Moyennes	16	16
	Extrêmes	4-27	4,8-32
D.I.N. (µmol.l^{-1})	Moyennes	55.14	21
	Extrêmes	20,7-136,1	2-41,5
D.R.P. (µmol.l^{-1})	Moyennes	13,87	1,2
	Extrêmes	0,1-20,9	0,3-2,9

vités industrielles et l'urbanisation en sont prioritairement responsables (Sfriso *et al.* 1989). Un autre trait important différencie les sites : les marées lunaires au Nord de l'Adriatique ont une grande amplitude (0,6 m en moyenne) conditionnant les échanges mer-lagune (Pirazzoli 1974, Pavoni *et al.* 1992) ; à Thau, au contraire, ces marées sont de faible amplitude (Millet 1989) et les échanges et variations de niveau (± 15 cm) sont essentiellement dus aux vents (De Casabianca & Kepel 1999).

Dans ce travail il nous a paru intéressant d'analyser, en parallèle dans ces deux milieux, la croissance des populations d'*U.rigida*. Celles-ci étant sujettes à un arrachement précoce, l'étude sera centrée au niveau des points de pousse.

MATÉRIEL ET MÉTHODES

Les sites de pousse sont situés à proximité de la mer où les populations d'*U.rigida* sont fixées : dans l'étang de Thau, au niveau principal du chenal de communication avec la mer, dans la lagune de Venise, près du Lido (Fig. 1).

Tous les facteurs environnementaux ont été mesurés à –1,5 m, tous les 10 jours en 1994-1995, dans les deux lagunes, avec une méthodologie comparable :

La température et la salinité sont mesurées *in situ* à l'aide de sondes électroniques de modèle WTW OXI 196, LF 196, à Thau, et HD 8705, Deta OHM, à Venise. La lumière incidente a été mesurée par photomètre dans les deux cas. Pour Venise, le photomètre est de type « Quantum-Radiometer-Photometer » (LI-Cor) portable. Pour Thau, ensoleillement journalier (J.cm^{-2}), communiqué par la station météorologique de Fréjorgues (France). Les radiations sont exprimées en PAR (Photosynthetic Active Radiation, µ E.m^{-2} s^{-1}). La formule utilisée (De Casabianca & Posada 1998) est : $I_c = [I_d/e^{(-k.p)}]$, où I_c = radiation incidente ; I_d = radiation journalière ; k = coefficient d'atténuation 0,5 correspondant à la cage ; e : exponentiel.

Les échantillons d'eau récoltés à –1,5 m ont été filtrés sur filtre Whatman GF/C pour déterminer la quantité de phosphore dissous réactif ($DRP = P - PO_4^{3-}$) et d'azote inorganique dissous ($DIN = N - NO_2^- + N - NO^-_3 + N - NH^+_4$) ($DIN = N\text{-}NO_2^- + N\text{-}NO_3^- + N\text{-}NH_4^+$) selon des méthodes colorimétriques de Strickland et Parsons (1972).

La biomasse d'*U.rigida* a été prélevée mensuellement (3 réplicats) en utilisant un cadre métallique (0,125 m^2 × 0,25 × 0,5 m) selon la méthode des quadrats permanents (Nienhuis 1978) à –1,5 m. Les Ulves recueillies ont été rincées, séchées à 60 °C pendant 24 h et pesées ; leur biomasse exprimée en kg PS.m^{-2} (PS : poids sec).

Le taux de croissance relative d'*U. rigida* est mesuré à partir d'une croissance en cage : de jeunes thalles de 10 cm fixés sont prélevés et déposés dans des cages disposées à –1,5 m. Après rinçage et essorage rapide, 3 lots de 50 g d'Ulves (w_i) à Thau et 200 g à Venise sont mis en place. Les cages (50x100 cm) ont un vide de maille de 1cm. Les algues sont récoltées au bout de 7 ou 10 j, pour être à nouveau pesées (w_f). Le taux de croissance relative (R.G.R : Relative Growth Rate), exprimé en pourcentage journalier est calculé selon la formule d'Evans (1972) : $R.G.R = [(\ln(w_i/w_f)/T]x100$; où w_i : poids initial (g) ; w_f :poids final (g) ; T : temps (jours).

Le traitement des données intégrant les paramètres physico-chimiques seuls (Température, Salinité, Lumière incidente, DIN et DRP à 1,5 m de profondeur) ainsi que ces mêmes variables et le R.G.R. ont été effectués par Analyse en Composante Principale (A.C.P.). D'autre part des courbes de variations saisonnières des variables physico-chimiques et biotiques ont été réalisées à partir des moyennes mensuelles.

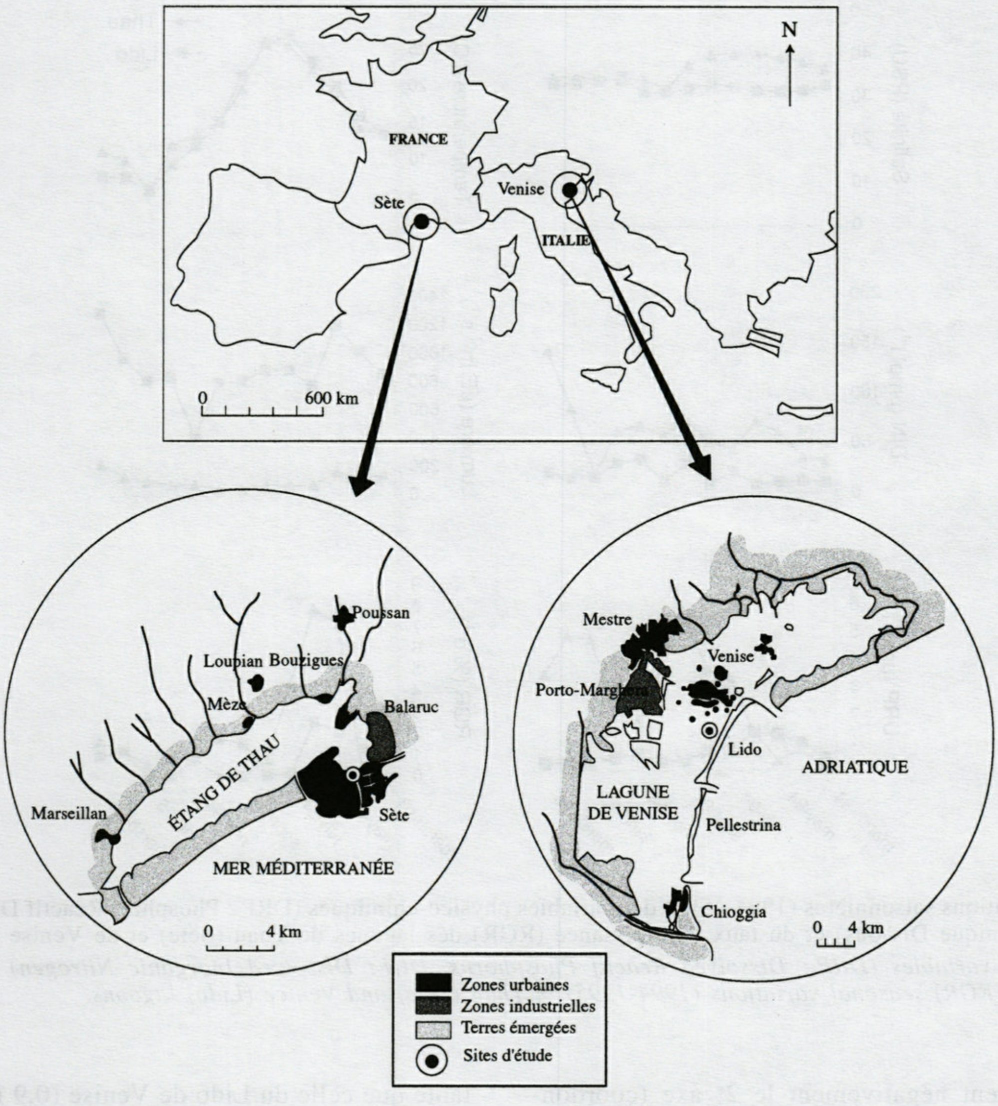

Fig. 1. – Les lagunes de Thau et de Venise. Localisation des sites d'étude (cercles).
Thau and Venice lagoons. Location of the sampling sites (circles).

RÉSULTATS

Variables environnementales

Variations saisonnières (Fig. 2).

Les températures de l'eau à Thau (Sète) et à Venise (Lido) sont voisines (avec des moyennes respectives de 16,07 °C et de 15,85 °C). Le minimum est atteint dans les 2 stations en janvier (6 °C) et le maximum en juillet (28 °C à Thau).

La lumière incidente au niveau des peuplements de la lagune de Venise (de 427 µ E $m^{-2}s^{-1}$ en novembre 94 à 1300 µ E m^{-2} s^{-1} en mars 95) est supérieure à celle reçue dans le bassin de Thau (43 µ E $m^{-2}s^{-1}$ en octobre à 227 µ E m^{-2} s^{-1} en mars 95).

La salinité moyenne des eaux de Thau (36,8 PSU) est supérieure à celle de la lagune de Venise (32,6 PSU). Les variations annuelles restent peu importantes dans les 2 lagunes (à Thau ± 8,1 PSU et à Venise ± 3,7 PSU).

La teneur moyenne en DIN du chenal de Thau (62 µ $mol.l^{-1}$) est supérieure à celle du Lido de Venise (17,9 µ $mol.l^{-1}$). Il en est de même pour celle des phosphates (DRP) : 2,79 $\mu mol.l^{-1}$; maximum : 5,79 $\mu mol.l^{-1}$ à Thau et 0,62 $\mu mol.l^{-1}$; maximum : 1,4 $\mu mol.l^{-1}$ à Venise.

Analyse en Composante Principale (Fig. 3)

A Thau, l'information portée par les axes 1 et 2 est respectivement de 34,9 et de 25,4 % (soit un total de 60,3 %). Salinité et température affectent positivement l'axe 1 (coordonnée 0,9 et 0,9) ; DIN et

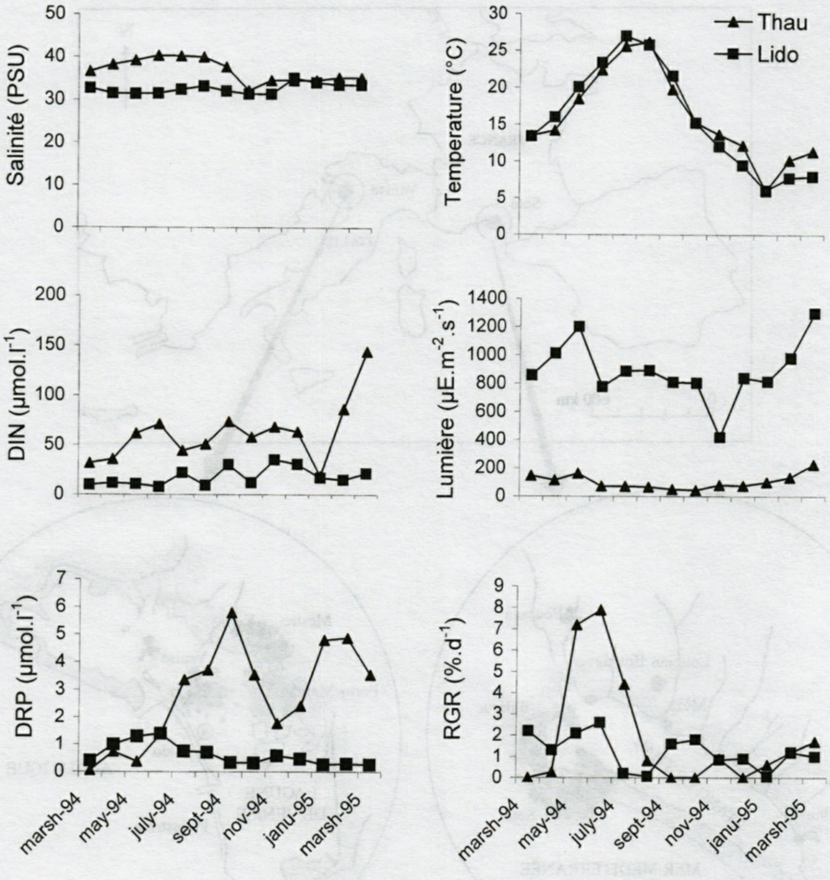

Fig. 2.– Variations saisonnières (1994-1995) des variables physico-chimiques (DRP : Phosphate Réactif Dissous, DIN : Azote Inorganique Dissous) et du taux de croissance (RGR) des lagunes de Thau (Sète) et de Venise (Lido).
Environment variables (DRP : Dissolved Reactif Phosphorus, DIN : Dissolved Inorganic Nitrogen) and relative growth rate (RGR) seasonal variations (1994-1995) in Thau (Sète) and Venice (Lido) lagoons.

DRP marquent négativement le 2^{e} axe (coordonnées respectives : –0,7 et –0,8). Le DIN est lié négativement avec l'axe 1 (coordonnée : –0.2). La lumière est faiblement représentée dans ce premier plan principal. Le coefficient de corrélation entre la salinité et la température est de 0,7.

Les variables hydrologiques de la station du Lido sont représentées à 56 % par le premier plan principal, le premier axe principal détient 34 % de l'information. On remarque que la salinité est bien représentée par l'axe 1 (coordonnée : 0,7). La lumière est fortement et négativement corrélée à l'axe 2 (-0,8). Dans la matrice des corrélations de ces variables la température est corrélée positivement avec le DRP ($R^2 = 0,3$), et négativement à la salinité ($R^2 = -0,4$).

Variables biotiques

Biomasse et taux de croissance

La biomasse (Fig. 4). d'*U. rigida* de la station de Thau (0,4 Kg PS.m^{-2}) est nettement moins importante que celle du Lido de Venise (0,9 Kg PS.m^{-2}). Le pic est atteint pour les 2 stations en juin. La biomasse diminue de juin à novembre à Thau ; à Venise on note un développement important à partir de septembre.

Le RGR moyen calculé sur l'année est de 1,2 %.j^{-1} à Venise et de 1,9 %.j^{-1} à Thau. Les courbes du RGR (Fig. 2) montrent de faibles valeurs (< 10 %.j^{-1}), et confirment l'existence de 2 pics équivalents (printemps et automne) à Venise et d'un pic important printanier à Thau, le second étant très peu marqué.

Analyse en Composante Principale (Fig. 5)

Dans l'ACP de Sète : 71 % de l'information est portée par les 2 premiers axes et 48,6 % par le premier. R.G.R., salinité, température et lumière sont bien représentés par l'axe 1 (coordonnées respectives = 0,6 ; 0,7 ; 0,7 ; 0,8). Le DIN est lié à l'axe 2 (coordonnée = 0,8). Le R.G.R est corrélé à la lumière ($R^2 = 0,6$) et plus faiblement à la température ($R^2 = 0,3$).

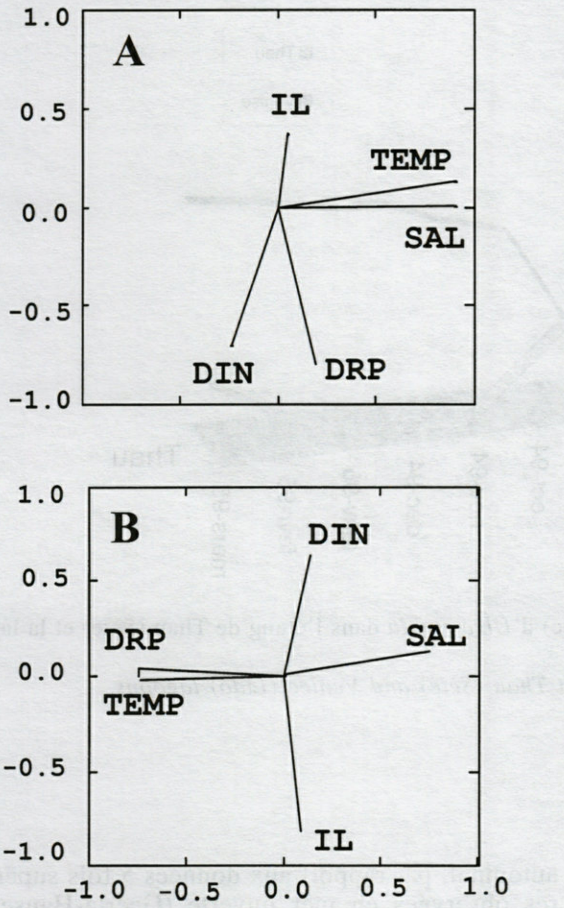

Fig. 3.– Analyses en Composantes Principales relatives aux variables environnementales : DIN (Azote Inorganique Dissous) ; DRP (Phosphore Réactif Dissous) ; IL (Lumière Incidente) ; SAL (Salinité) ; TEMP (Température) à –1,5 m de profondeur, dans l'étang de Thau (A) et la lagune de Venise (B).
Principal Componant Analysis of main environment factors: DIN (Dissolved Inorganic Nitrogen); DRP (Dissolved Reactif Phosphorus); IL (Incident Light); SAL (Salinity); TEMP (Temperature) at –1,5 m depth, in the Thau (A) and Venice (B) lagoons.

Dans l'ACP du Lido : les variables étudiées sont expliquées à 28 % par le premier axe et à 21 % par le deuxième. Le R.G.R est fortement et négativement lié à l'axe 2 (coordonnée = – 0,8). A noter, la corrélation entre R.G.R. et DRP (R^2 = 0,3).

DISCUSSION

Les résultats relatifs aux variables environnementales concernent la corrélation entre salinité et température (ACP de Thau), et celle entre DRP et température (ACP de Venise). Dans l'étang de Thau qui subit un faible renouvellement d'eau, la température augmente en même temps que la salinité du fait de l'évaporation. La lagune de Venise sujette à marées, ne connaît pas le même phénomène ; le rôle du phosphate y apparaît par contre, mettant en évidence le relargage à partir des sédiments lié à la montée thermique (Callame 1961), élément confortant les résultats antérieurs (De Casabianca *et al.* 1997) et à Venise (Sfriso *et al.* 1987, 1988).

Le pic de biomasse observé dans le site de Thau est relativement bas (0,85 Kg ps.m^{-2} contre 1,69 Kg ps.m^{-2} dans le site de Venise), ce qui contraste avec le RGR (supérieur à Thau). En fait, il faut considérer les valeurs de Thau comme correspondant strictement à une biomasse d'algues jeunes et fixées à leur support, ce qui n'est pas entièrement le cas ni pour Venise ni pour les données citées par ailleurs, jusqu'à 10 fois supérieures, mais qui représentent une biomasse accumulée par les courants souvent très loin des sites de pousse (Riouall 1976, De Casabianca 1989, Piriou *et al.* 1989, Sfriso 1989, Dion & Le Bozec 1996).

Les données de RGR sont donc plus rigoureuses car elles sont réellement la résultante de l'effet des variables environnementales du lieu considéré. L'examen de leur évolution saisonnière révèle ici, à Thau comme à Venise, une courbe bimodale dont les deux pics (printanier et automnal), sont équilibrés à Venise contrairement à Thau où le second est peu marqué. Ce shéma méridional bimodal s'oppose au shéma classique unimodal nordique (Sand-Jensen & Borum 1991, Geertz-Hansen & Sand-Jensen 1992, Geertz-Hansen *et al.* 1993, Malta & Verschuure 97). La courbe de biomasse décrite en Espagne (Romero *et al.* 1996) nous donne raison. Si la phase descendante de la courbe « nordique » a été souvent expliquée par une limitation de l'azote, il est clairement démontré aujourd'hui que l'évolution saisonnière de la température en est prioritairement responsable, les températures < 10 ° et > 23 °C limitant le développement de l'algue (De Casabianca & Posada 1998). Il apparaît nettement ici que les températures élevées sont responsables de la dépression estivale du RGR, comme il est bien clair que le shéma unimodal ne se produit que dans les milieux où la température excède rarement 20 °C ; les « marées vertes » pouvant alors s'y produire avec intensité et durée.

Il n'est pas question de faire ici le procès de l'azote qui est indispensable au développement de l'Ulve et dont l'importance a été en particulier soulignée par l'analyse des contenus de l'algue (Rivers & Peckol 1995, Viaroli *et al.* 1992, 1993) ; et de son niveau critique (Hernandez *et al.* 1997) ; mais en milieu constamment eutrophisé, il est bien difficile de démontrer quoi que ce soit dans ce sens (Sfriso 1995, Sfriso & Marcomini 1997).

Un autre facteur important, la lumière incidente, peut expliquer la faiblesse des valeurs de RGR de Thau (< 10 %.j^{-1}), et particulièrement celle du pic

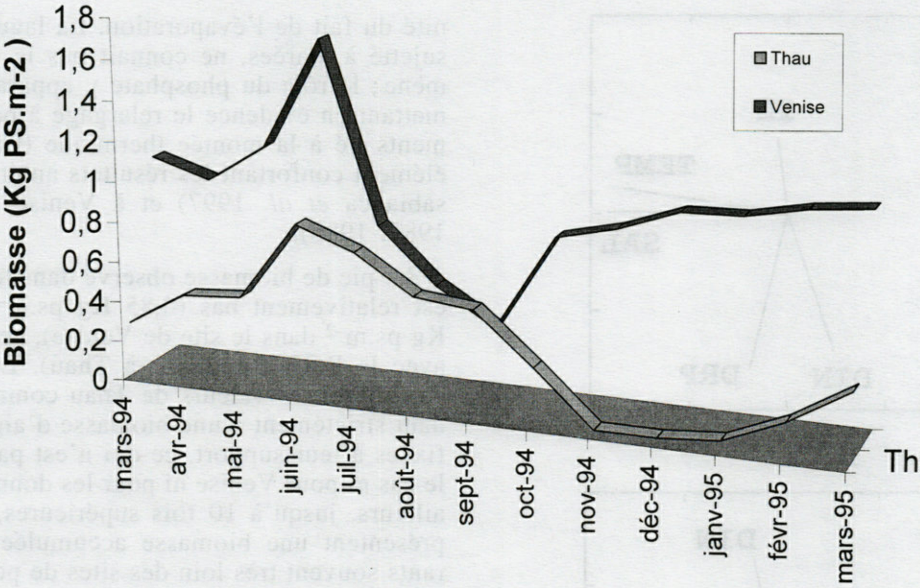

Fig. 4.– Variations saisonnières de la biomasse (PS : poids sec) d'*Ulva rigida* dans l'étang de Thau (Sète) et la lagune de Venise (Lido).

Ulva rigida *biomass (PS: dry weight) seasonal variations in Thau (Sète) and Venice (Lido) lagoons.*

automnal, par rapport aux données 5 fois supérieures observées en mer ouverte (Geertz-Hansen & Sand-Jensen 1992) ; les valeurs lagunaires sétoises (42-227µ E m^{-2}s^{-1} contre 427-1300µ E m^{-2}s^{-1} au Lido de Venise) sont en effet inférieures aux besoins de l'Ulve en lumière (400-500µ E m^{-2}s^{-1} d'après Ramus 1983).

Le pic automnal de Thau est éliminé par la turbidité des eaux (la dégradation estivale étant suivie d'un pic de phosphate puis de phytoplancton provoquant une restriction de lumière au niveau des peuplements) (De Casabianca *et al* 1997a). Ceci corrobore les mesures de Vergara *et al.* (1998) au niveau des peuplements. Donc, malgré des conditions thermiques symétriques à celles du printemps, le pic du RGR automnal de Thau se trouve réduit par manque d'intensité lumineuse. Notons, par contre, que deux pics équivalents sont observés

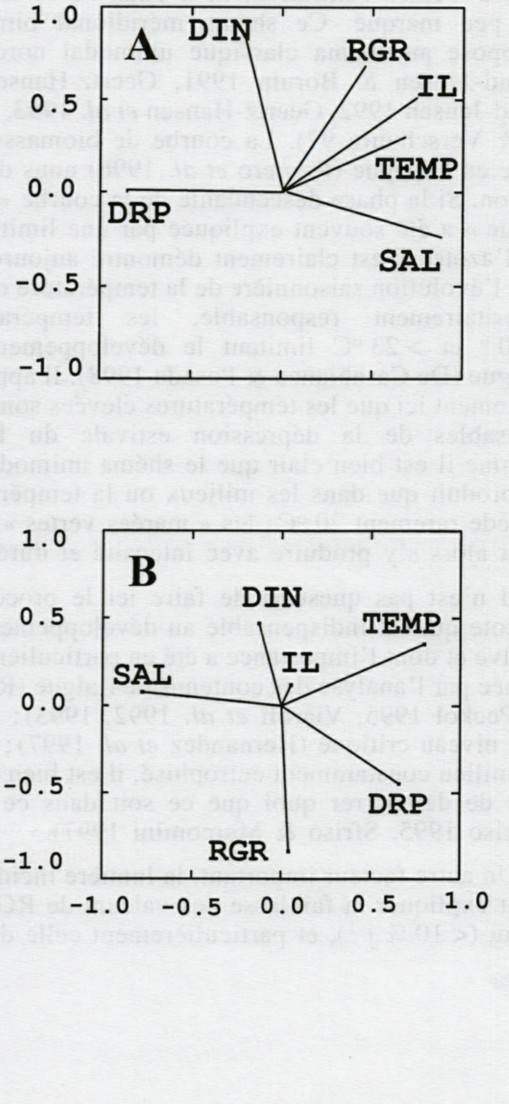

Fig. 5.– Analyses en Composantes Principales des variables environnementales (DIN = Azote Inorganique Dissous ; DRP = Phospore Réactif Dissous ; IL = Lumière Incidente ; SAL = Salinité ; TEMP = Température) et du taux de croissance relative (RGR) d'*Ulva rigida* dans l'étang de Thau (A) et la lagune de Venise (B).

Principal Componant Analysis of the main environmental variables (DIN = Nitrogen; DRP = Dissolved Reactif Phosphorus; IL = Incident Light); SAL = Salinity); TEMP = Temperature) and Relative Growth Rate (RGR) of Ulva rigida *in Thau (A) and Venice (B) lagoons.*

à Thau chez la Rodophycée *Gracilaria bursa-pastoris* Gemlin (Silva) (De Casabianca *et al* 1997b), dont les besoins en lumière (9,6-100µ E $m^{-2}s^{-1}$) sont inférieurs à ceux de l'Ulve. L' A.C.P. relative au RGR confirme ces résultats par une corrélation R.G.R/lumière. Donc, dans l'étang de Thau, où la turbidité de l'eau est plus importante que dans la lagune de Venise et où les sels nutritifs (DIN et DRP) sont présents en quantité supérieure aux besoins de l'algue, la lumière est le facteur limitant.

Un point reste à expliquer : la faiblesse du RGR de Venise que ni la lumière incidente, ni l'azote, ni la biomasse mise en cage, ne peuvent expliquer. Deux variables peuvent intervenir : – 1) la qualité des Ulves mises en culture (thalles jeunes encore fixés à forte potentialité à Thau, fragments libres pouvant être plus âgés à Venise. – 2) la limitation en DRP des eaux du Lido. Jamais observée dans le Nord de l'Europe (Ryter & Dunstan 1971), l'ACP de Venise confirme cette hypothèse au Lido. Dans cette station où l'eau est claire et renouvelée, la teneur en DRP faible, apparaît comme le facteur limitant du développement d'*U. rigida.*

On conclut donc à l'importance des facteurs physiques (température et lumière) en milieu eutrophisé.

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DIATOMS AND DATABASES – A SHORT REVIEW

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DIATOMS
DATABASES
TAXONOMY
ECOLOGY
CODED LIST
CD-ROM
WEB PAGE
INTERNET

ABSTRACT. – It is becoming increasingly obvious that the transmission of information is crucial in the global scientific context. One only has to think of the consultation of type specimens from a diatom herbarium or the verification of an identification through electronic consultation of a photographic library. Computerized databases on diatoms could become indispensable tools supporting taxonomic uniformity. We are highlighting some advance in the field of electronic archiving diatom information and this should be regarded only as a short review. Examples are taken from various countries who have created electronic databases on diatoms. At the beginning of this new millennium, we will assist in a proliferation of websites devoted to diatom research. If we work together, we can develop the basis for a new era of research in diatomology, accord greater importance to computerizing the databases and ensuring their transmissibility to our colleagues all over the world.

DIATOMÉES
BASES DE DONNÉES
TAXONOMIE
ÉCOLOGIE
LISTE DE CODES
CD-ROM
PAGE WEB
INTERNET

RÉSUMÉ. – Il devient de plus en plus évident que la transmission d'information est primordiale dans le contexte scientifique global. Il suffit de penser tout simplement à la consultation des spécimens types d'herbier de Diatomées ou encore à la vérification d'une identification par la consultation d'une photothèque par voie électronique. Des bases informatisées sur les Diatomées peuvent devenir des outils indispensables permettant de supporter une uniformité taxinomique. Cet article se veut une brève revue des bases de données existantes sur les Diatomées et, pour cette raison, nous avons surtout mis en évidence les récents avancements technologiques dans le domaine de l'archivage électronique de données sur les Diatomées. Des exemples ont été puisés dans divers pays qui ont créé de telles bases de données électroniques sur les Diatomées. À l'aube de ce nouveau millénaire, nous allons assister à une prolifération de sites électroniques voués aux Diatomées. En travaillant ensemble, il nous sera possible d'élaborer les fondements d'une nouvelle ère de recherche en diatomologie, d'accorder une part plus importante à l'informatisation des bases de données et d'en assurer la transmissibilité auprès de nos collègues du monde entier.

INTRODUCTION

With the relentless advance of computer technology, it is becoming increasingly evident that transmissibility of information is crucial in the global scientific context. This is all the more true, as research teams are becoming not only multidisciplinary but multinational as well. Attention to this important topic from the current debate on diatom research was first drawn by a Roundtable that took place during the 18th Colloquium of the Association des Diatomistes de Langue Française held in Nice, France, on 14-17 September 1999 (Poulin *et al.* 2000). The relevance of maintaining diatom databases, the harmonization of data sets and the transfer of information have been recognized as being beneficial to the scientific community. Therefore, this paper highlights some of the advances in the field of electronic archiving diatom information available under various formats and for diverse purposes. Bare in mind that the scope of this paper is far to encompass an exhaustive review of the topic but instead wants to start a dialogue and, for this reason, it has to be seen as a short review.

CLASSIFICATIONS

One only has to think of the consultation of type specimens of a diatom herbarium or the verification of an identification through electronic consultation of a photographic library. Also to be remembered are the corresponding databases where the abiotic parameters of a given ecosystem are preserved. Computerized databases on diatoms could become indispensable tools supporting a kind of taxonomic uniformity even where there are differing classifications. For example, there is no reason why names valid under one school or another could not be kept; in any event, the information can be conserved in synonymy. In fact, Pullan *et al.* (2000) developed a model named, *Prometheus Taxonomic Model*, for representing taxonomic data in a flexible and dynamic electronic system capable of handling and comparing multiple simultaneous classifications. The model separates the process of nomenclature from that of classification, and enables the system to store multiple classifications. A prototype system is presently being tested on some groups of vascular plants and the latest information can be obtained via the Prometheus website (www.dcs.napier.ac.uk/~prometheus). On a more general point of view, databases would also make it possible to incorporate measurements of physicochemical parameters so that the autecology of the diatoms in question could be better described and understood.

GEOGRAPHICAL AND ECOLOGICAL DATABASES

In Canada, for instance, an initial attempt at computerizing the national phycological collection was begun by the Canadian Museum of Nature towards the middle of the 80s but was interrupted in early 1991, which seriously compromised the progress of this project. The system used, *CURATOR*, was developed from a special software program to manage the national natural history collections with an integrated geographical atlas and a taxonomic dictionary. By the time this software was abandoned, nearly 40 % of the phycological collection had been entered into that system. Recently a database for the diatoms of the northern hemisphere's circumpolar regions containing over 300 lakes in the Yukon, Siberia, Northern Quebec and Labrador was established by R. Pienitz of the Université Laval (Quebec City, Canada) and will be soon available on Internet. This database contains species names of diatoms that have been so far recorded from these circumpolar regions, and the accuracy of their identification is currently being verified. In addition to these taxonomic data, there are measurements of the physicochemical parameters of the water bodies that were studied, for example, temperature, oxygen levels, pH, conductivity, phosphorus and nitrogen, to mention only a few.

TAXONOMY AND SOFTWARES

The establishment of databases to help in the identification of diatoms has also aroused much interest in the last decades (Cairns *et al.* 1982, Droop *et al.* 1993, Williams 1993, Johnson & Lowe 1995). At the beginning of the 90s, a database and a computer-assisted identification program for marine protists were developed by Estep *et al.* (1989, 1992, 1993). The computer software, called *Linnaeus Protist,* is available on compact disk. It contains information on 312 marine protists (microalgae and protozoans) from northern European marine coastal waters. From a main menu, users may obtain information on particular diatom species that includes line drawings, descriptions, references, and in most cases, on-screen, photograph-quality micrographs. From a main menu, the user can access various other files, including taxonomic keys, distribution maps of toxic and blooming species, and a master list of species. This CD-ROM is a valuable educational tool for both the classroom and the field laboratory.

At about the same time, other developments were happening worldwide. In France, the software program *OMNIDIA* (http://perso.club-internet.fr/clci/) was developed to assist the rapid calculation of diatom indices as well as offering the users with a possibility to archive photomicrographs of diatoms monitored (Lecointe *et al.* 1993, 1999). The database, currently available on *OMNIDIA*, was created in 1981 by the Cemagref in Bordeaux from the need to codify the designations of diatom species used in establishing the index approach, and it is regularly updated. The last edition of the software contains a photographic library of 209 freshwater diatoms accurately identified from river systems of French departments.

Numerous new species have been described since the publication of the last volume of VanLandingham's Catalogue (VanLandingham 1967-1979) as well as a high number of taxonomic revisions have been proposed (Krammer & Lange-Bertalot 1986, 1988, 1991a, b, Round *et al.* 1990). To make it easier to work through the labyrinth of new or recent taxonomic designations, the *OMNIDIA* base attempts to make a few non-exhaustive additions to the catalogue of VanLandingham (1967-1979) in the form of abridged records, even an index. Since the number of publications consulted is relatively limited, the resulting gaps are necessarily significant. The file nonetheless reviews most of the classic publications in which new diatoms are generally described (e.g., *Bacillaria, Diatom Research, Diatom, Arch Hydrobiol, Bibl Diatomol, Iconogr Diatomol, Nova Hedwigia, Phycologia, Canadian Botany, Europ J Phycol, Proceedings* of international seminars) and most of the works or monographs devoted to diatoms. Of course, the synonymies already mentioned in the catalogues of Mills (1933-1935) or VanLandingham (1967-1979) do not necessary appear there and the database does not in any way claim to substitute for them. It is only a modest stop gap measure designed for computer use, while awaiting the re-publication and updating of these works.

TAXONOMIC ENCODING

Numerous proposals for coding algae, and diatoms in particular, can be found in various authors (e.g., Fabri & Leclercq 1984, Droop *et al.* 1993, Williams 1993, Whitton *et al.* 1998). They were designed for different purposes, including collection management, taxonomy, morphological variability or even the codification of autecological data of fossil and recent diatoms, and they generally make use of complex codifications consisting of 5 to 8 codes (sometimes up to 15), associating either numbers (Whitton *et al.* 1978, 1979, Denys & Lodewijckx 1984, Güttinger 1986-1998, Williams *et al.* 1988, Denys 1991, Whitton 1991, Whitton *et al.* 1998), or letters (Klasvik 1974, Fabri & Leclercq 1984, van Dam *et al.* 1994), or numbers and letters (de Wolf 1982).

A simplification of computerized entry operations consisted in the use of 4-letter codes developed for the *OMNIDIA* database. Four-letter codes are easy to read, particularly using ecological data analysis programs such as multivariate statistics (Lecointe *et al.* 1993, Prygiel & Coste 1999). It is strongly recommended that a common codification system be adopted to facilitate exchanges and possible confrontations among the data inventoried and so that index methods can be more readily standardized.

NATIONAL PROJECTS

In France, beginning in the year 2000, the results of the diatom indices obtained from the Réseau National de Bassin will be centralized by the Réseau National des Données sur l'Eau in agreement with the Service d'Administration National des Données Relatives à l'Eau, an organization that is developing a common language for data concerning water and is establishing data standardization to make the definition and exchange of data among producers, users and databanks both compatible and homogenous. Recent developments lead us to believe that the Agence de l'Eau Artois-Picardie will take care of the diatom monitoring and indices for France while the Muséum National d'Histoire Naturelle in Paris will manage and conserve the raw diatom material and permanent slides (J Prygiel, pers comm). In addition, a free software program on compact disk *(TAX'IBD)* for identifying diatoms selected for calculating the Indice Biologique Diatomées or *IBD* (Lenoir & Coste 1996, Prygiel & Coste 1999) is now available and 700 copies have been reproduced and distributed through France by the water agencies (Prygiel & Coste 2000).

In Switzerland, a database was created in 1999 with the support of regulatory agencies such as the Office Fédéral de l'Environnement, de la Forêt et du Paysage in Bern, the AquaPlus' office in Unterägeri and the Office Cantonal de Protection des Eaux of Zürich, as well as professional Swiss diatomists. The database archives all data and information available on river diatoms from Switzerland in order 1) to bring together existing and usable raw data in a unique collection (diatom and physicochemical data), 2) to facilitate data comparison, 3) to complete observations in regions where data and information are lacking, and 4) to calibrate existing indices and develop one or more indices for Switzerland in terms of its various geological basins and in agreement with national regulations regarding water quality objectives.

For this project, the taxonomic and nomenclature base reference was limited to the use of the *Süsswasserflora* (Krammer & Lange-Bertalot 1986, 1988, 1991a,b) and five critical volumes from the series *Bibl. Diatomol.* (Krammer & Lange-Bertalot 1985, Lange-Bertalot 1993, Lange-Bertalot & Krammer 1987, 1989) and *Iconogr. Diatomol.* (Lange-Bertalot & Metzeltin 1996). For the raw database on Swiss diatoms, accessibility problems have not yet been resolved, because each canton remains the owner of the raw data that it has provided. Access to such data must be discussed on a case by case basis. In addition, the AquaPlus bureau has developed programs to access and validate these data, but this part of the database is private. The AquaPlus bureau and, in particular, J. Hürlimann (joachim.huerlimann@aquaplus.ch) are available, however, for any follow-up question or for any proposal to participate in joint projects related to this databank.

EUROPEAN PROJECTS

At the European level, Droop *et al.* (1993) are currently working on the Automatic Diatom Identification And Classification *(ADIAC)* project which seeks to develop algorithms allowing for the automatic identification of diatoms through information obtained from illustrations, for example, size and ornamentation. Further information on the *ADIAC* project can be obtained from M. Bayer at the Royal Botanic Garden in Edinburgh (http://www.rbge.org.uk/ADIAC).

The European Diatom Database *(EDDI)* is another information system that is allowing diatom-based palaeoenvironmental reconstruction for pH, total phosphorus and salinity. It makes possible to gather and harmonize European data on diatoms and water chemistry in order to ultimately produce a CD-ROM and a website making available the combined data as well as photomicrographs of the main diatom taxa and software for data analysis. More information can be obtained at the website (http://www.geog.ucl.ac.uk/ecrc/eddi/).

Another European project, *PAEQANN* (http://www-cesac.cemes.fr/~paeqann/), consists in developing general methodologies based on advanced modelling techniques (mainly goal function and artificial neural networks) for predicting structure and diversity of key aquatic communities (diatoms, macro-invertebrates and fish) under natural and human-induced disturbances. The development of predictive models for aquatic ecosystem variability will contribute to create a comparative common base at the European scale and an overall appreciation of the water resources in Europe.

Species lists and iconography

It is important not to overlook all the websites or webpages that have been created in the last ten years. The project of Fourtanier & Kociolek (1999) lists the 1001 genera of diatoms (http://www.calacademy.org/research/diatoms/genproject) and proposes a description and illustration of 73 freshwater genera (http://www.calacademy.org/research/diatoms/genera/index.html). Recently, P. Compère, of the Jardin Botanique National de Belgique, made available on the website of the Association des Diatomistes de Langue Française or ADLaF (http://perso.club-internet.fr/clci/diatom-ADLaF.htm) the first identification key in French for all freshwater genera (http://perso.club-internet.fr/clci/ADLaF_Cle_des_genres.htm). In Australia, diatomists have proposed also an illustrated key to the common genera of freshwater diatoms (www.arts.monash.edu.au/ges/research.Cpp/Diatoms/generic.html). For the marine sector, it is interesting to consult the taxonomic list of phytoplankton of Skagerrak-Kattegat on the website of M. Kuylenstierna and B. Karlson (www.marbot.gu.se/SSS/SSShome.htm).

CONCLUSION

There are numerous websites that provide images of microscopic organisms for the purpose of ecological monitoring of harmful species of algae or illustrations showing the biological diversity of microalgae. In any case, the fact remains that, at the beginning of this new millennium, we will see a proliferation of websites devoted to diatoms. A list of the most important websites on diatom databases is summarized in Table I, which will be maintained on the *ADLaF* webpage and regularly updated. It is becoming increasingly crucial that we work together with research centres and organizations in the field of diatomology. With technological progress, we can now, directly from the microscope, preserve the image of the diatom that we are examining and transfer it to our personal computer or even send it electronically to a distant colleague. This is what lies in store for the new generation of diatom specialists.

But there is one crucial difficulty in this vision; no one wants to be the leader either because of diverging work objectives or for want of funds. However, there could be some light at the end of this tunnel. It would be sufficient if a dialogue were initiated with museological institutions to have them take on the task of preserving data on diatoms. A situation that recently evolved with the Muséum National d'Histoire Naturelle in Paris being considered the repository organization for all diatom material and slides originating from the monitoring of the French rivers. Is this not in any case one of the fundamental missions of a museum ? They should not only make science accessible to the general public, but should also participate in preserving our natural heritage by archiving their collections, computerizing them and disseminating them. A computerized collection is a collection that can be accessible to users; it is, as it were, alive. If a museum is most often defined as a centre of expertise on biodiversity, this must be widely disseminated to the public. Whence the interest presented by diatom databases that would include, for example, illustrations, descriptions, reference documents, distribution maps and measurements of the corresponding physicochemical parameters.

Unfortunately, we are still far from having such tools, but if we work together, we can develop the basis for a new era of research in diatomology, accord greater importance to computerizing the databases and ensuring their transmissibility to our colleagues all over the world.

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Table I. – Websites on diatom databases and on general information on diatom research.

Internet databases on diatoms (site addresses)	European project	Taxonomic database	Iconography database	Species list (checklist)	Genera list (checklist)	Diatom palaeoecology	Methods/Techniques	Geographical data	Environmental data	Bibliography data	Software on diatoms	Cultures diatoms database	Genetic database	Diatomist Association	International news groups	General Diatom Home page	E-mail & addresses data	Meetings & courses
http://www.rbge.org.uk/ADIAC/	x	x	x	x												x		
http://www.rbge.org.uk/ADIAC/db/Adiacgen.htm			x	x	x													
http://www.rbge.org.uk/ADIAC/db/adiacdb.htm			x	x	x													
http://www.rbge.org.uk/ADIAC/pubdat/prepro.html#1							x											
http://www.geog.ucl.ac.uk/ecrc/eddi/	x		x			x		x	x							x		
http://www-cesac.cemes.fr/~paeqann/	x	x		x				x	x									
http://www.indiana.edu/~diatom/dpdc/dpdc.html						x												
http://www.geog.ucl.ac.uk/ecrc/edgis/edgis.htm								x	x									
http://www.kv.geo.uu.se/inqua/news2/nl2-dfc.htm		x				x			x		x							
http://www.kv.geo.uu.se/inqua/news19/n19-ehj.htm		x	x			x		x	x									
http://www.nmnh.si.edu/ing/		x			x					x								
http://www.nmnh.si.edu/cgi-bin/wdb/ing/names/form		x			x													
http://www.bgbm.fu-berlin.de/iapt/ncu/genera/NCUGQuery.htm		x			x													
http://128.32.109.44/e-ina.html		x		x	x													
http://www.arts.monash.edu.au/ges/research/Cpp/Diatoms/			x	x	x		x			x				x				
http://www.msu.edu/~kirschte/biovol/											x							
http://perso.club-internet.fr/clci/			x								x							
http://206.67.72.201/catalog/np/jan95np/DATA/3-540-14502-8.html											x							
http://perso.club-internet.fr/clci/ADLaF_Cle_des_genres.htm					x													
http://megasun.bch.umontreal.ca/gobase/													x					
http://www.awi-bremerhaven.de/Biomeer/molekulargenetische-e.html													x					
http://www.calacademy.org/research/diatoms/					x							x				x		
http://www.calacademy.org/research/diatoms/genera/index.html			x		x													
http://www.calacademy.org/research/diatoms/genproject/					x													
http://www.umich.edu/~mongolia/index.html			x	x						x						x		
http://www-personal.umich.edu/~asalger/HomePage/Home.html			x	x												x		
http://www.umich.edu/~phytolab/GreatLakesDiatomHomePage/glspeciesok2.html			x	x												x		
http://www.nwl.ac.uk/~loissys/algal_coded_list.htm		x		x														
http://www.marbot.gu.se/SSS/SSShome.htm			x	x				x										
http://www.math.ualberta.ca/~bowman/diatom/			x	x														
http://www.umich.edu/~phytolab/GreatLakesDiatomHomePage/top.html			x	x	x													
http://www.bgsu.edu/departments/biology/algae/index.html			x	x														
http://seaweed.ucg.ie/search/default.html		x	x							x								
http://hjs.geol.uib.no/diatoms/Marbles/index.html-ssi			x															
http://www.weizmann.ac.il/home/crosta/Diat.html			x															
http://www.fxbrowne.com/html/micro/diatom.html			x															
http://www.mnhn.fr/mnhn/geo/diatoms/index.htm			x						x									
http://www.schweizerbart.de/j/										x								
http://www.koeltz.com/										x								
http://www.balogh.com/~balogh/										x								
http://www.serv.net/~mallard/diatom/diatom_biblio.html										x								
http://ccmp.bigelow.org/												x						
http://www.bgsu.edu/Departments/biology/algae/html/DiatomCulture.html				x								x						
http://www.ife.ac.uk/ccap/												x						
http://www.gwdg.de/~epsag/phykologia/catalogue/gatt_99/bacillo.htm												x						
http://www.bio.utexas.edu/research/utex/genus/genus.html												x						
http://www.ocgy.ubc.ca/projects/nepcc/diatoms.htm												x						
http://www.botany.utoronto.ca/utcc/list.stm												x						
http://www.bio.utexas.edu/research/utex/reference/reference.html										x								
http://www.indiana.edu/~diatom/diatom.html						x	x			x		x		x	x	x		x
http://www.isdr.org/										x				x		x		x
http://www.bgbm.fu-berlin.de/diatoms/default.htm																		x
http://perso.club-internet.fr/clci/diatom-ADLaF.htm					x					x				x		x	x	x
http://seaweed.ucg.ie/algae-l/default.html															x		x	
http://listserv.indiana.edu/archives/diatom-l.html															x		x	
http://www.indiana.edu/~diatom/members.txt																	x	
http://seaweed.ucg.ie/cost/MicroAlgalCultures.html												x					x	
http://seaweed.ucg.ie/cost/AlgalHerbaria.html																	x	
http://www.calacademy.org/research/diatoms/nads/nads.htm																		x

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MORPHOLOGICAL RUDIMENTATION AND NOVELTIES IN STYGOBITIC CIROLANIDAE (ISOPODA, CYMOTHOIDEA[1]

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ISOPODA CIROLANIDAE
STYGOBITIC/MARINE SPECIES
RUDIMENTATION ("REGRESSION")
EVOLUTIONARY NOVELTIES
HYPOGEAN LIFE ADAPTATION

ABSTRACT. – The diversity of cirolanid isopods, all of marine origin, in subterranean aquatic habitats, is remarkably high, 68 species being presently recognized (in 19 genera). These stygobites display, in clear contrast with the marine (i.e., non-subterranean) cirolanids numerous cases of rudimentation ("regression") but also a number of remarkable morphological and other evolutionary novelties, some of them unique in Isopoda, or even in Crustacea. Rudimentation and novelties are the two components of troglomorphy, sometimes the limit between them being not sharp. These cases are examined under the following headings: body shape; depigmentation and tegumental smoothness; absence of "molariform spines"; anophtalmy; elongation and slenderness of appendages; development of tactile (mechanoreceptory) equipment; development of chemosensors ("olfactory organs"); rudimentation and novelty in uropods; rudimentation and novelty in pleopods; some particular structures in hypogean species; the propodial organs; volvation; paedomorphy; facts related to "K-strategy". Study of this array of facts contributes to a better understanding of adaptation to hypogean life. In the introductory notes are briefly expressed the author's opinions about mechanisms considered as underlying rudimentation and novelties respectively as responses to hypogean life, and about preadaptation considered as an essential notion for understanding colonization of the Stygal, this being well exemplified by Cirolanidae. The remarkable diversity of morphological and other adaptive traits of stygobitic Cirolanidae could be explained by the fact that the hypogean aquatic environment is much more complex than seen by traditional biospeology, animals displaying a great variety of adaptive responses in order to cope with the constraints of this complex, rigorous environment.

ISOPODA CIROLANIDAE
ESPÈCES STYGOBIES / MARINES
RUDIMENTATION ("RÉGRESSION")
NOUVEAUTÉS ÉVOLUTIVES
ADAPTATION À LA VIE HYPOGÉE

RÉSUMÉ. – La diversité des Isopodes Cirolanides – tous d'origine marine – dans les eaux souterraines est remarquablement grande, 68 espèces stygobies appartenant à 19 genres étant actuellement connues. Ces espèces montrent – contrairement aux Cirolanides marins, épigés – de nombreux cas de rudimentation ("regression") mais aussi un nombre de remarquables nouveautés évolutives (morphologiques ou autres) parfois uniques chez les Crustacés. Rudimentation et nouveautés sont les deux aspects de la troglomorphie, la limite entre ceux-ci étant parfois peu distincte. Ces cas sont examinés aux titres suivants: habitus; dépigmentation et absence d'ornementation tégumentaire; absence d' "épines molariformes"; anophtalmie; allongement et gracilité des appendices; développement des phanères tactiles (mécanorécepteurs); développement des organes chémorécepteurs, ou "olfactifs"; rudimentation et nouveautés dans la morphologie des uropodes; rudimentation et nouveautés dans celle des pléopodes; autres structures particulières propres aux espèces hypogées; organes propodiaux; volvation; paedomorphose; certains faits en relation avec la "stratégie K". L'examen de tous ces faits peut contribuer à une meilleure compréhension du phénomène de l'adaptation au milieu souterrain. Dans l'introduction sont brièvement exprimées les opinions de l'auteur sur les mécanismes considérés comme pouvant déterminer rudimentation et nouveautés en tant que résultat de la vie hypogée, ainsi que sur la préadaptation considérée comme notion essentielle pour comprendre la colonisation du Stygal (ceci étant bien illustré par le cas des Cirolanides). La remarquable diversité des particularités adaptatives – morphologiques et autres – des Cirolanides stygobies pourrait être expliquée par le fait que le domaine aquatique souterrain est beaucoup plus complexe qu'il l'a été longtemps considéré par la biospéologie, les stygobies faisant montre d'une grande variété de réponses adaptatives afin de faire face aux contraintes de ce milieu complexe et rigoureux.

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[1] Concerning use of the suborder name Cymothoidea Dana, 1852 instead of the widely used Flabellifera: see, i.a., Racovitza, 1912: 213-215, and Wägele, 1989: 162-163.

INTRODUCTION

The problem of adaptation to hypogean life has been addressed in numerous publications; but the aim of the present paper is definitely not a review of published information on this topic. Being neither a geneticist, nor a science philosopher, I shall tackle the problem from the point of view of a taxonomist and biospeologist. Nevertheless, I feel compelled to briefly express my views on a few general aspects.

Despite the fact that Cirolanidae are a group of isopod crustaceans having much to tell in this respect, they have not received the deserved attention. Presently some 360-370 species of marine (not subterranean) Cirolanidae are described. From subterranean aquatic habitats presently not less than 68 validly recognized species are described in 19 validly recognized genera, plus five subspecies of three of the species. These stygobitic genera will be here listed: *Antrolana* Bowman, *Arubolana* Botosaneanu & Stock, *Bahalana* Carpenter, *Cirolana* Leach (sg. *Cirolana* and sg. *Anopsilana* Paulian & Delamare Deboutteville), *Cirolanides* Benedict, *Creaseriella* Rioja, *Faucheria* Dollfus & Viré, *Haptolana* Bowman, *Marocolana* Boutin, *Metacirolana* Nierstrasz, *Mexilana* Bowman, *Skotobaena* Ferrara & Monod, *Speocirolana* Bolivar y Pieltain, *Sphaerolana* Cole & Minckley, *Sphaeromides* Dollfus, *Turcolana* Argano & Pesce, *Typhlocirolana* Racovitza, *Yucatalana* Botosaneanu & Iliffe, *Zulialana* Botosaneanu & Viloria. All their species are fully troglomorphic, adapted to the hypogean mode of life, whereas quite a few (3 species in the genera *Annina* Budde – Lund and *Saharolana* Monod) are stygophiles possibly on route to colonizing the subterranean realm. The ratio hypogean/marine species is thus remarkably high in this group of isopods.

The stygobites, belonging to rather diverse lineages, are unanimously considered as derived from marine ancestors, but almost nothing is known about the possible ancestors. They inhabit a vast array of subterranean aquatic habitats (Botosaneanu *et al.* 1986).

For the present paper the main information sources on marine Cirolanidae were the comprehensive publications by Bruce (1986), Kensley & Schotte (1989), and Brusca *et al.* (1995). In order to avoid tedious repetition, etc., the genera of marine species which will be quoted in the text are here listed: *Annina* Budde-Lund, *Bathynomus* Milne Edwards, *Booralana* Bruce, *Cartetolana* Bruce, *Cirolana* Leach (sg. *Cirolana* and sg. *Anopsilana* Paulian & Delamare Deboutteville), *Conilera* Leach, *Dolicholana* Bruce, *Eurydice* Leach, *Excirolana* Richardson, *Limicolana* Bruce, *Metacirolana* Nierstrasz, *Natatolana* Bruce, *Neocirolana* Hall, *Oncilorpheus* Paul & Menzies, *Orphelana* Bruce, *Parabathynomus* Barnard, *Politolana* Bruce, *Pseudolana* Bruce, *Seychellana* Kensley & Schotte, *Xylolana* Kensley.

I prefer "rudimentation" to "regression", "reduction", or "degeneration" used in the literature; and "novelties" to "acquisitions" or "elaborated features". Obviously, rudimentation and novelties are the two components of troglomorphy (troglobiomorphy). In publications, much more attention has been paid to "regressions" than to "acquisitions", which is definitely an error (Botosaneanu & Holsinger 1991), and one aim of the present paper is to demonstate how numerous and conspicuous the evolutionary novelties displayed by stygobitic animals can be. In fact, the limit between the two aspects is not sharp: rudimentation is, too, evolutionary novelty, and it has a possible adaptive significance – something postulated in several publications. Of course, troglomorphy has reached quite different degrees and modes of expression in various taxa.

Rather much has been published on the mechanisms on which rudimentation and novelties – as responses to hypogean life – depend (one example: the special issue of the NSS Bulletin – J Caves and Karst Studies 47 (2) 1995). Several authors (e.g. Kosswig 1965, Wilkens 1973) have stressed the role of genetic drift and accumulation of neutral mutations, or that of pleiotropy, in the induction of "regression", a role for natural selection being retained only for "acquisitions". Others (e.g. Heuts 1953) have – in my opinion rightly – stressed the role of natural selection even for "regression". Whereas some (Hobbs III, 1998: 895) argue that the question simply cannot be at present answered. Various interesting ideas have been formulated in this context: adaptive value of the "reduction" processes; competitive success of "reduced" phenotypes in the hypogean environment, possibly caused by accompanying physiological improvement not morphologically detectable; the "energy economy hypothesis" stressing the importance of quantity and quality of energetical resources of the environment in induction and degree of rudimentation.

I believe that the antagonism between the two main opinion streams (*v. supra)* is unjustified: clearly, development of any organ– and in any direction – is *genetically* governed; and, clearly, animals are *selected* for life in the quite special subterranean realm. I cannot refrain from quoting a graduate student of my late colleague J.H. Stock (Van den Bosch 1988) who, after thoroughly reviewing – with a fresh mind – the literature devoted to meaning and mechanisms of eye regression, concluded that the discussion could be explained rather by "riding one's hobby" than by factual difference.

I consider preadaptation an essential notion for understanding the colonization by animals of subterranean habitats. In terms like "exaptation" or "adoption" I see a good deal of tautology. Botosaneanu & Holsinger (1991) have criticised in some detail underestimation of the importance of preadaptation for subterranean biology. The term "preadaptation" was created by L. Cuénot and refined by him during the 1st half of past century (Guyon 1995); in 1951, Cuénot defined it as "selection of preadapted animals", a telling formula. But his idea that, once a species is adapted, it cannot "go towards more adaptation" is wrong, in my opinion: it certainly can, by accentuating characters already present in the preadapted species, and by creating novelties in accordance with the characteristic features of the colonized habitat of the (quite heterogeneous) Stygal. According to Simpson (1944) preadaptation cannot achieve much in the absence of further refining of characters by selection; commenting on this, Guyon (1995) writes: "La préadaptation est donc pour Simpson étroitement encadrée en amont et en aval par la sélection naturelle".

For understanding something about Cirolanidae preadapted for hypogean life, there is nothing more instructive than reading paragraphs devoted to habitats in publications on marine cirolanids, where these are very often described as burrowing in sand, in mangrove mud, in coral reef sediments, or living under rocks, in algal turfs or in kelp holdfasts, in the chamber of sponges or in vacant burrows of various animals, in crevices of coral rock, dead wood bored by *Sphaeroma* or *Teredo,* dead mangrove roots, or in dense mussel or barnacle beds. Not only life in such cryptic habitats and burrowing behaviour, but sometimes also anophtalmy or eye rudimentation, a smooth cuticula, and various degrees of depigmentation, characterize subterranean-preadapted marine cirolanids in genera like *Cirolana*, *Eurydice*, *Metacirolana*, *Natatolana*, *Orphelana*, *Pseudolana*. But it should be stressed that only quite seldomly morphological novelties found in stygobitic Cirolanidae have been found in marine species characterized as preadapted by their habitat, behaviour, eye rudimentation, or depigmentation.

FACTS, AND TENTATIVE EXPLANATIONS

Body shape

No generalization is possible about body shape of the stygobitic cirolanids beyond stating that species inhabiting groundwater in porous habitats are definitely more slender than some of those living in subterranean water in karstic environments. Nevertheless, it is a fact that a series of stygobitic species, belonging to genera like *Antrolana, Cirolanides, Mexilana, Turcolana, Typhlocirolana,* or *Speocirolana* (Fig. 1-2) are more slender than most marine species with their stout, strongly domed, often strongly widened body. Even in the rare marine species with body much longer than the greatest width (some *Eurydice,* species of the small genera *Conilera*, *Oncilorpheus,* or *Xylolana*), the somewhat "clumsy" shape is striking. Clearly, the difference fades when very large cave species like *Speocirolana bolivari* (Rioja, 1953) or *Zulialana coalescens* Botosaneanu & Viloria, 1993, are considered. Racovitza (1912: 247) observes, about body lenghtening in *Typhlocirolana*, that it is possible that this character "... ne soit pas dû à la vie cavernicole et qu'il ait été hérité de l'ancêtre lucicole. Beaucoup de Cirolanides épigés le possèdent également. Peut-être est-ce un caractère de lignée qui s'est seulement exacerbé depuis la colonisation souterraine".

Depigmentation, tegument smoothness

All stygobitic cirolanid species are entirely depigmented (cuticula devoid of chromatophores) in contrast with the marine species where practically always at least some chromatophores are present even if the body is described as "white" or "whitish" (quite a few exceptions are mentioned for species of *Natatolana* like *N. bowmani* Bruce, 1986, or *N. thurar* Bruce, 1986; but in such cases conservation in formalin could be the explanation). Some integumental pigment is retained in stygophile species: *Saharolana seurati* Monod, 1930, or *Annina lacustris* Budde – Lund, 1908 (situation unknown for *A. fustis* Bowman & Iliffe, 1991).

All stygobitic species have the cuticula of cephalon, pereion, pleon, and pleotelson smooth, and often thin; in some cases it is so thin as to become translucent, allowing easy observation of pleopods and of most of the internal anatomy (this peculiarity is particularly impressive in species of *Bahalana).* In contrast, in marine species very often a relief ornamentation (tubercles, ridges...) is present, and sometimes strongly developed: species of *Cirolana (Anopsilana*), *C. (Cirolana*), *Metacirolana;* whereas species of *Oncilorpheus* are characterized by a negative sculpture on the pereional dorsum. A well developed relief ornamentation characterizes also the stygophile *Annina lacustris;* this is much reduced in the equally stygophilic *A. fustis* which has probably reached a more advanced degree of subterranean adaptation.

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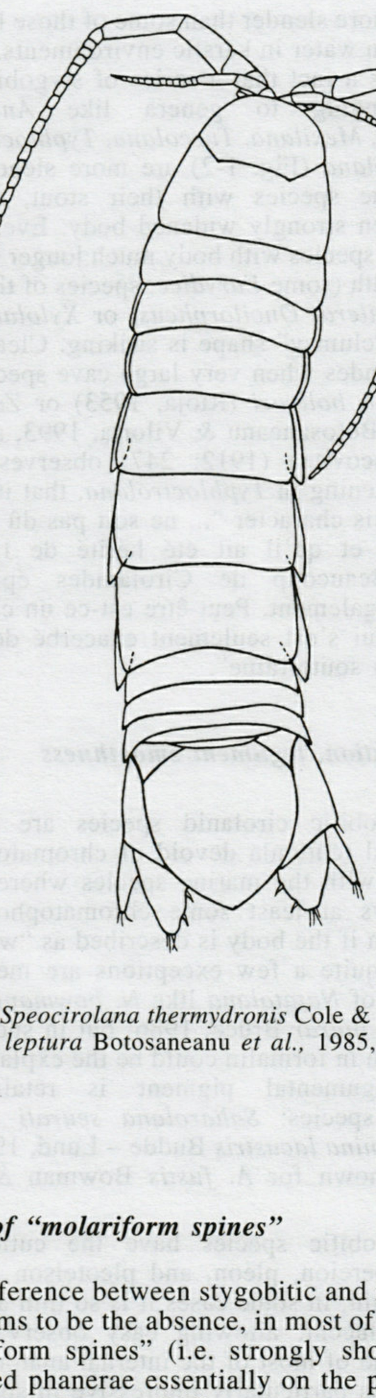

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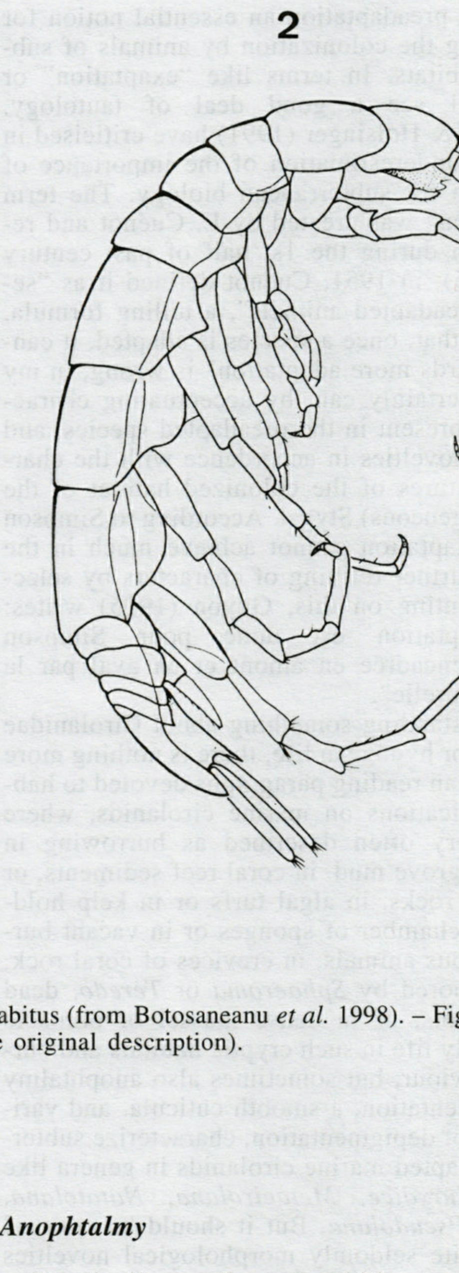


Fig. 1. – *Speocirolana thermydronis* Cole & Minckley, 1966, habitus (from Botosaneanu *et al.* 1998). – Fig. 2. – *Typhlocirolana leptura* Botosaneanu *et al.*, 1985, habitus (from the original description).

Rarity of "molariform spines"

A difference between stygobitic and marine species seems to be the absence, in most of the first, of "molariform spines" (i.e. strongly shortened and thickened phanerae essentially on the palmar margin of pereiopods I-III and especially of the gnathopods) sometimes found in marine species in several genera. Of course, there is extreme diversity in shape of spines on the pereiopods of stygobitic cirolanids, but they practically always conserve the "spiniform" aspect lost in the "molariform spines" (an exception is represented by the "blunt tubercles" on the gnathopod merus of species in the lineage *Typhlocirolana – Turcolana – Marocolana).* Genus *Anopsilana,* including both stygobitic and epigean species, is particulary demonstrative in this respect, all marine species having molariform spines which are absent in all stygobitic species.

Anophtalmy

Practically all stygobitic species are anophtalmous, without any trace of ommatidia or eye pigment. An exception is the interstitial micro-oculate *Arubolana parvioculata* Notenboom, 1984. Micro-oculate is, too, the stygophile *Saharolana seurati,* whereas in *Anopsilana conditoria* Bruce & Iliffe, 1992, mention is made of presence of "indistinct cuticular traces of ocelli". It may be added that in species of *Annina* the eyes have "a non-facetted gap separating dorsal and ventral parts" (Bowman & Iliffe 1991). About marine genera with species displaying various degrees of eye rudimentation: see Introduction.

Elongation and slenderness of appendages

Rightly considered as a compensatory element for sight loss, appendage elongation and slender-

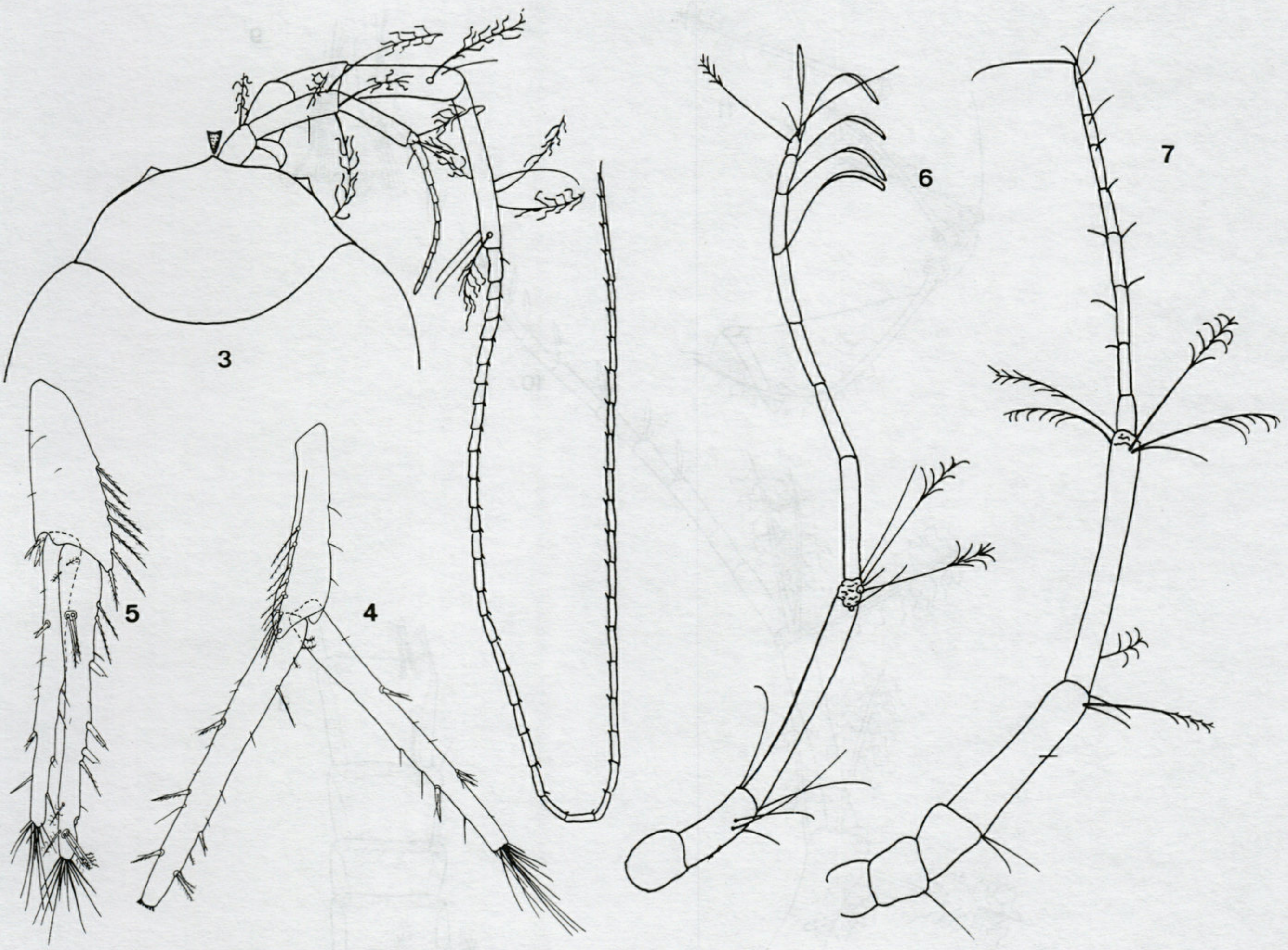


Fig. 3. – *Speocirolana disparicornis* Botosaneanu & Iliffe, 1999, cephalon with A I and A II (from the original description). – Fig. 4-5. – *Typhlocirolana leptura* Botosaneanu *et al.*, 1985, right uropod of ♀ and left uropod of ♂ (from the original description). – Fig. 6-7. – *Yucatalana robustispina* Botosaneanu & Iliffe, 1999, left A I and A II (from the original description).

ness is very often exemplified in biospeological publications. It is frequently found in appendages of stygobitic Cirolanidae, and here I give only a small selection of examples.

The extraordinary slender and elongate uropod rami in both sexes of the phreatic species *Typhlocirolana leptura* Botosaneanu *et al.*, 1985, from Morocco (Fig. 4-5) is unequalled in marine or stygobitic Cirolanidae – although uropods with slender rami are present in other *Typhlocirolana*. *Speocirolana disparicornis* Botosaneanu & Iliffe, 1999, from a Mexican karstic spring and cave, is characterized by extremely long AII almost reaching to the end of the pleotelson (Fig. 3). In *Yucatalana robustispina* Botosaneanu & Iliffe, 1999, from cenotes in Yucatan, both subequal AI and AII (Fig. 6-7) are, although not very long, extremely slender, of a type possibly never present in marine species.

Generally speaking, there are often striking differences between the development of antennulae and antennae in hypogean and marine species, the most impressive ones being displayed by AI. Quite frequently, marine species have strongly shortened, mostly plump antennulae with sometimes strongly compressed flagellar articles, of a type clearly unknown in any subterranean species. In some marine species also the antennae are strongly shortened (as in species of *Cartetolana, Booralana, Cirolana (Cirolana), Conilera, Natatolana;* the most impressive case being, maybe, that of *Orphelana perplexa* Bruce, 1981); in some others, only AI belongs to this type whereas AII are not strongly shortened (*Dolicholana,* or some *Natatolana),* being sometimes even very long *(Eurydice,* some *Natatolana).*

Development of tactile (mechanoreceptory) equipment

In some stygobitic species impressive bundles of simple setae from adjacent alveolae are inserted on peduncular and flagellar articles of AII. This was

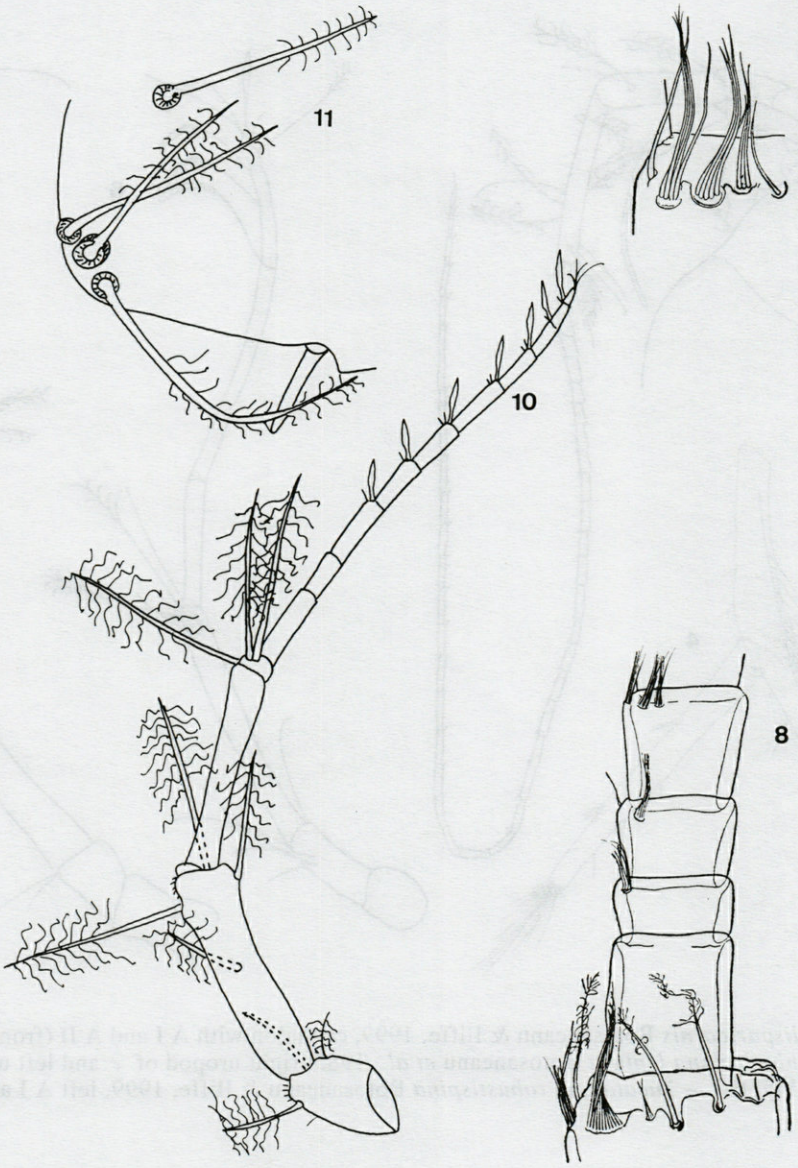
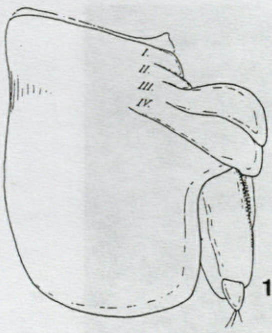


Fig. 8-9. – *Sphaeromides bureschi* Strouhal, 1963, left A II, distal part of article 5 of peduncle and flagellum articles 1-4; and distal part of 7th flagellum article (from the original description). – Fig. 10-11. – *Speocirolana disparicornis* Botosaneanu & Iliffe, 1999, left A I, and apex of uropod endopodite, dorsal view (from the original description).

well illustrated, i.a., for *Sphaeromides bureschi* Strouhal, 1963 (Fig. 8-9), as well as for species as diverse as *Anopsilana cubensis* (Hay, 1903), *Haptolana somala* Messana & Chelazzi, 1984, *Marocolana delamarei* Boutin, 1993, *Skotobaena monodi* Ferrara & Lanza, 1978, *S. mortoni* Monod, 1972, *Turcolana ruffoi* Argano, 1996, or *Zulialana coalescens*. It is a tempting idea that such formations are tactile novelties compensatory for sight loss; however, they have been, too, illustrated for various marine species, such as – to quote two extreme cases – *Excirolana mayana* (Ives, 1891) – where the AII of adults are described (Brusca *et al. 1995) as "brushlike antennae" – or Oncilorpheus jerrybarnardi* Brusca *et al.*, 1995.

On the other hand it seems certain that the equipment of plumose and palmate setae – certainly the most efficient type of mechanoreceptory setal equipment – is better developed in subterranean than in epigean Cirolanidae. This is valid, at least in many cases, for AI and AII peduncles (Fig. 10: AI of *Speocirolana disparicornis* is instructive in this respect). But even more striking is the fact that the equipment of plumose and palmate setae of the uropods is by far richer in the stygobites (although it cannot be excluded that some details were not always adequately described or illustrated in the marine taxa). One thing is particularly impressive: on the dorsal face of the uropod endopodite of most – or all – stygobites



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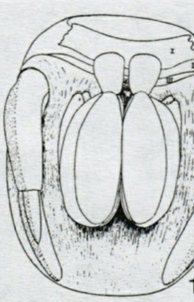

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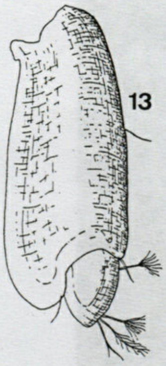

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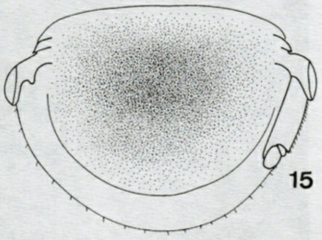

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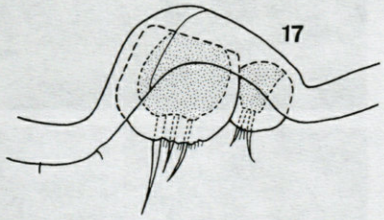

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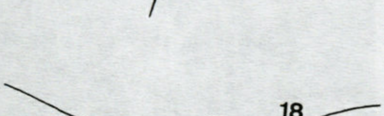

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Fig. 12-13. – *Faucheria faucheri* (Dollfus & Viré, 1900), pleon and pleotelson with uropod, lateral view; and right uropod, dorsal view (from Racovitza 1912). – Fig. 14. *Skotobaena mortoni* Monod, 1972, pleon and pleotelson with the uropods, ventral view (from the original description). – Fig. 15-16. – *Zulialana coalescens* Botosaneanu & Viloria, 1993, pleon and pleotelson with left uropod, ventral view; and right uropod, ventral view (from the original description). – Fig. 17-18. – *Sphaerolana affinis* Cole & Minckley, 1970, and, respectively *S. interstitialis* Cole & Minckley, 1970, distal parts of uropod, strongly magnified (from Botosaneanu *et al.* 1998).

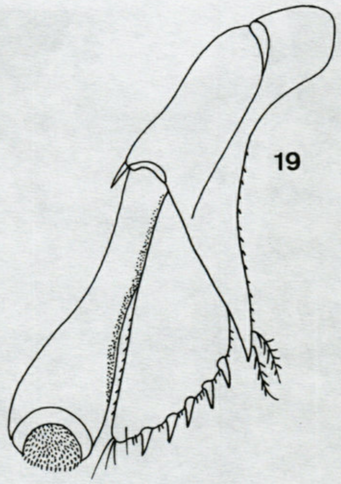

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Fig. 19. – *Speocirolana fustiura* Botosaneanu & Iliffe, 1999, left uropod (from the original description).

there is at least one, but there are often two or several swinging palmate setae (sometimes called "tiges acoustiques") in 1 to 4 groups, sometimes inserted on what was probably rightly described as well delimited "sensory patches". Their presence was ascertained, for instance, in *Arubolana, Cirolana* (*C.*) *troglexuma* Botosaneanu & Iliffe, 1997, *C. (C.) pleoscissa* Botosaneanu & Iliffe, 1997, *Haptolana, Marocolana, Speocirolana, Sphaeromides, Turcolana, Typhlocirolana, Yucatalana, Zulialana*. Fig. 11 represents the powerful dorsal equipment of swinging palmate setae from strong alveolae near the endopodite apex of the uropod of *Speocirolana disparicornis*.

Development of chemosensors ("olfactory organs")

It could be supposed that the equipment of chemoreceptor organites will prove to be richer in the stygobites than in the marine species (something having been advocated, for instance, for Decapoda). Actually, the reverse seems to be true (like for instance in some Ostracoda). They are, indeed, rather well or even well developed on the flagellum of AI and AII of many subterranean – adapted species; and some marine species were illustrated (correctly ?) with a poor equipment of chemoreceptors. However, in a very large number of marine species – the genera relevant in this respect being *Cartetolana, Cirolana* (*Anopsilana*), *C. (Cirolana), Eurydice, Excirolana, Metacirolana, Natatolana, Neocirolana, Pseudolana* – this equipment is remarkably rich on the flagellum of AI and often on that of AII, sometimes in many or all species of a genus; and sometimes they form true rows on various articles, something only in exceptional cases seen in a subterranean cirolanid (*Haptolana trichostoma* Bowman, 1966). Generally speaking, it seems that for marine Cirolanidae more powerful chemoreceptor systems are necessary than for the fresh– or brackish water subterranean species. But it should be kept in mind that there exists published evidence (discussion in Wägele 1992: 592-593) that the chemoreceptors on AI and AII have differ-

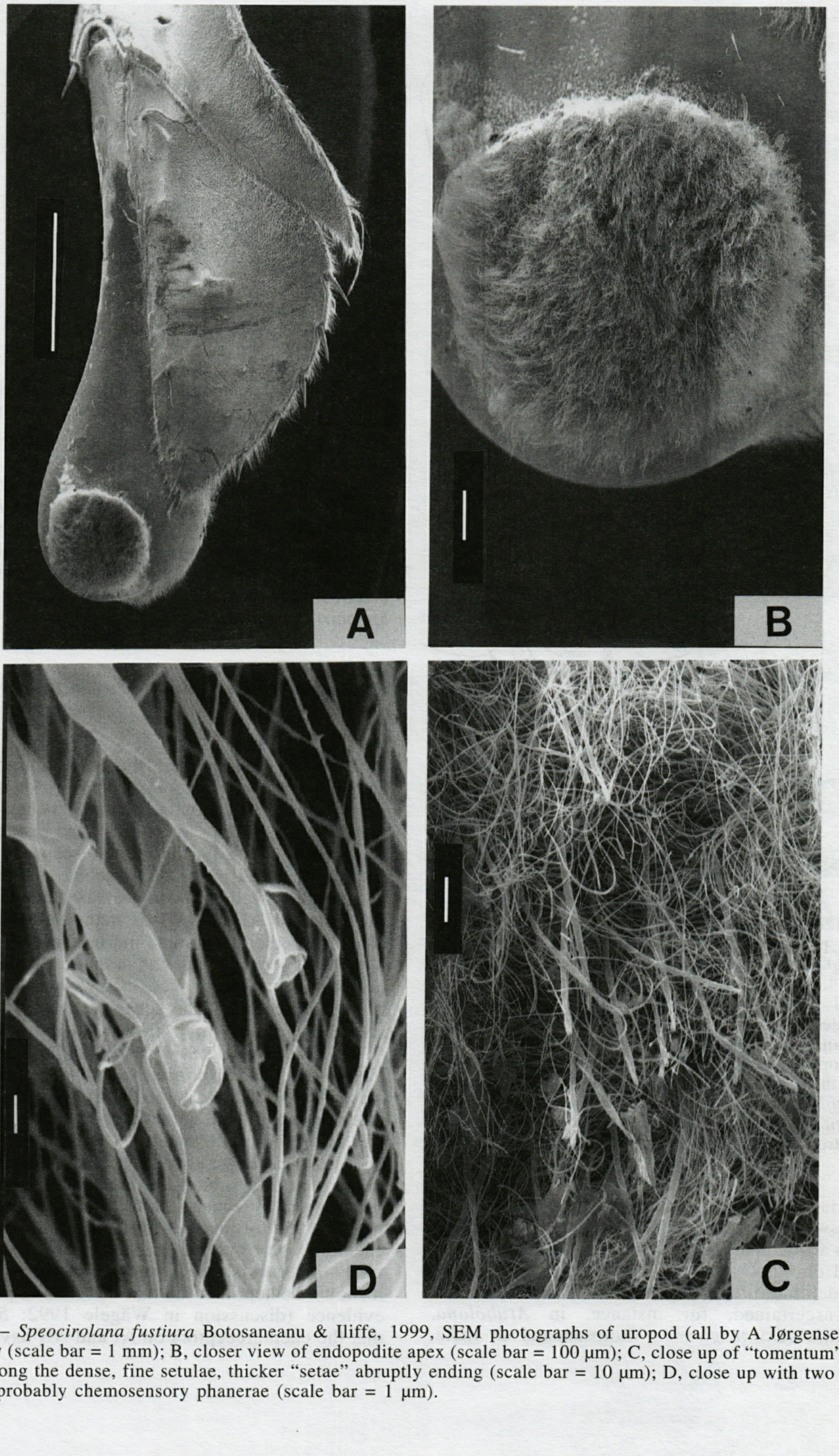


Fig. 20. – *Speocirolana fustiura* Botosaneanu & Iliffe, 1999, SEM photographs of uropod (all by A Jørgensen). A, overview (scale bar = 1 mm); B, closer view of endopodite apex (scale bar = 100 µm); C, close up of "tomentum", showing among the dense, fine setulae, thicker "setae" abruptly ending (scale bar = 10 µm); D, close up with two blunt, hollow, probably chemosensory phanerae (scale bar = 1 µm).

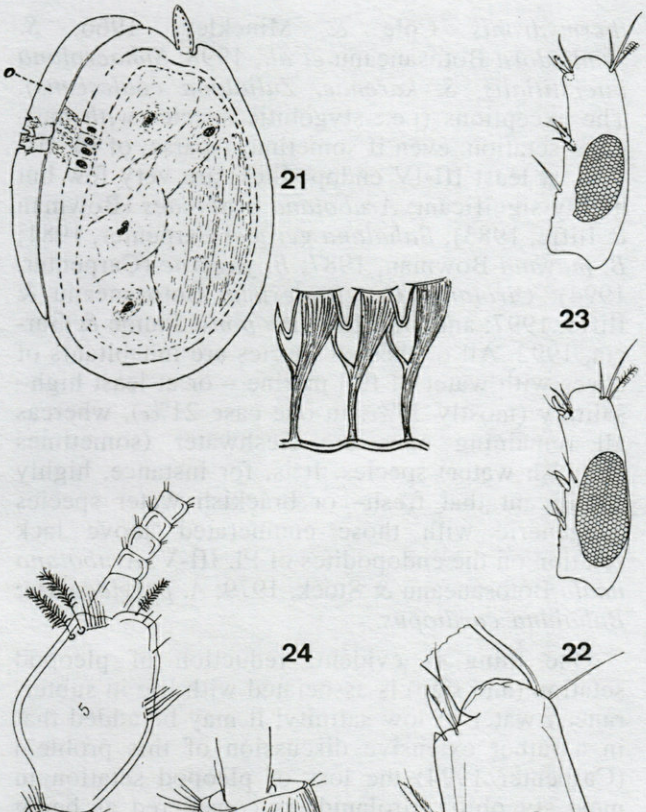


Fig. 21. – *Typhlocirolana buxtoni* Racovitza, 1912, transverse section through the propodus of PII; O = the propodial organ; small appended figure: more strongly magnified detail from section through propodial organ (from the original description). – Fig. 22. – *Turcolana steinitzi* (Strouhal, 1960), propodus of PII, ♂, with propodial organ (from the original description). – Fig. 23. – *Turcolana adaliae* Botosaneanu & Notenboom, 1989, ♂, propodus of PII (below) and of PIII (above), with propodial organs (from the original description). – Fig. 24. – *Sphaeromides polateni* Angelov, 1968, male A II peduncle with first articles of flagellum, and ventral view of article 5 of peduncle (from the original description).

ent origins and functions, only those on AI being long-distance chemoreceptors (aesthetascs), whereas the sensilla on AII are "contact chemoreceptors" sensitive to chemical and mechanical stimuli. It should also be added that in some stygobitic species (*Yucatalana robustispina*: Fig. 6; *Cirolana (Anopsilana) yucatana* Botosaneanu & Iliffe, 2000) there are very long aesthetascs on the last flagellar articles of A1, and that this remarkable length (and, thus, surface) may represent a counterpoise for the low number of aesthetascs.

Rudimentation and novelty in uropods

In practically all marine cirolanids the uropods are functional, movable, steering appendages normally developed in all their parts (in species of *Excirolana* – see, i.a., Brusca *et al.* 1995: Fig. 48, etc. – the short uropod endopodite has a curious notch – or "pit" – on its lateral margin, but I do not believe that this can be considered as incipient rudimentation).

In contrast, in several hypogean genera and species belonging to quite different lineages (discussion in Botosaneanu & Viloria 1993) various modes and degrees of uropod rudimentation are found, representing some of the most impressive morphological characteristic features induced by hypogean life. Only cases of advanced rudimentation will be mentioned here, but it should be kept in mind that in a series of other stygobitic Cirolanidae the uropods, although "normal" looking, are hard, calcified appendages capable only of restricted motion.

In *Skotobaena mortoni* from caves in Ethiopia, the hard, almost ankylosed uropods almost devoid of setation (Fig. 14) follow the lateral margins of the pleotelson, being at the same time twisted towards the median line in such a manner that the strongly reduced and hollowed exopodites acquire a ventral position; the uropods are in such a way placed as to form with the pleotelson a deep ventral chamber for the small pleopods, and they cannot be observed dorsally. The situation is practically identical in *S. monodi* from wells in southern Somalia (Ferrara & Lanza 1978); in *Faucheria faucheri* (Dollfus & Viré, 1900) from karstic habitats in southern France, the situation is similar in several respects, but here only one small branch (the endopodite ?) is appended to the very strong, certainly ankylosed sympodite (Fig. 12-13). In *Zulialana coalescens* from a cave in NW Venezuela, the completely ankylosed uropods rooted in the axilla of the 3d pleonal epimeres, are extremely small (2.4 times shorter than the pleotelson), but both rami are still distinct, although the exopodite is extremely reduced (Fig. 15-16). The fact deserves mention that also in *Speocirolana disparicornis* the uropods (Botosaneanu & Iliffe 1999: Fig. 49, 68) are completely concealed under the strongly vaulted pleotelson; but they are well developed and seemingly freely movable, although probably not very efficient steering appendages. Finally, an extreme degree of modification and rudimentation is displayed by all 3 species (all Mexican) described in *Sphaerolana*: *S. affinis* Cole & Minckley, 1970; *S. interstitialis* Cole &

Minckley, 1970 (for these 2 species see also Botosaneanu *et al.* 1998); and *S. karenae* Rodriguez-Alm. & Bowman, 1995. In all three the sympodite is relatively very large, with exceedingly small rami in *S. affinis* and *S. karenae,* and with one of them (which ?) having disappeared in *S. interstitialis* (Fig. 17-18).

A most extraordinary situation is that found in a species discovered in small pools at the bottom of a deep Mexican cave: *Speocirolana fustiura* Botosaneanu & Iliffe, 1999. Here, sympodite and endopodite of the ankylosed uropods have no very peculiar shape, whereas the exopodite is transformed in a way completely unknown in Cirolanidae, being a long, hard, club-shaped appendage with a round apical zone completely covered by what can be superficially described as a dense tomentum (Fig. 19; there is tomentum also along the median face of the exopodite). Thanks to the kindness of R.M. Kristensen and to the ability of A. Jørgensen, SEM photographs can be presented (Fig. 20) revealing a significant feature: at high magnifications (Fig. 20 C,D) among the very dense, thin setulae covering the round apical zone (and, in fact, each composed of about 3 even thinner, plaited filaments which unwind finally), some much thicker ones become apparent, approximately 25 µm long, ending abruptly, and hollow. According to R.M. Kristensen (in litt.) such hollow formations are an indication for chemoreception, as known from other crustaceans. Uropods with a chemosensory function are clearly an evolutionary novelty in Cirolanidae.

In all these cases complete loss of the ability of the uropods to function as steering appendages is evident. As documented in several publications this is in direct relation with the small bodies of water available, and sometimes also with the highly unstable hydrological regime. In my opinion another mechanism working in parallel could be involved, as response to life in such an environment: a shift from actively searching for living prey in the water mass, to scavenging on the bottom.

Rudimentation and novelty in pleopods

In a vast majority of stygobitic cirolanids, and even in a stygophilous species such as *Saharolana seurati,* the endopodites of pleopods III-V are devoid of marginal setation (something seen only in very few marine species, according to Bowman & Franz 1982). Moreover, in some stygobitic species the endopodites of *all* pleopods are without marginal setation and often of small size, in some of them even the setation of the exopodites, or at least of some of them, being very reduced or absent (cases of more accentuated rudimentation of setation: *Mexilana saluposi* Bowman, 1975, *Skotobaena monodi, S. mortoni, Speocirolana thermydronis* Cole & Minckley, 1966, *S. zumbadora* Botosaneanu *et al.*, 1998, *Sphaerolana interstitialis, S. karenae, Zulialana coalescens).* The exceptions (i.e.: stygobitic species *with* marginal setation, even if sometimes sparse, of Pl. III-V or at least III-IV endopodites) are very few but highly significant: *Arubolana aruboides* (Bowman & Iliffe, 1983); *Bahalana geracei* Carpenter, 1981; *B. mayana* Bowman, 1987; *B. yagerae* (Carpenter, 1994); *Cirolana (C.) troglexuma* Botosaneanu & Iliffe, 1997; and *Metacirolana ponsi* Jaume & Garcia, 1992. All of these 6 species are inhabitants of caves with water of full marine – or at least high–salinity (mostly 35‰, in one case 21‰), whereas all remaining ones are freshwater (sometimes brackish water) species. It is, for instance, highly significant that fresh– or brackish water species congeneric with those enumerated above lack setation on the endopodites of Pl. III-V: *Arubolana imula* Botosaneanu & Stock, 1979; *A. parvioculata; Bahalana cardiopus.*

One thing is evident: reduction of pleopod setation (and size) is associated with life in subterranean water of low salinity; it may be added that in a rather extensive discussion of this problem (Carpenter 1994) the loss of pleopod setation in most stygobitic cirolanids is considered as being more associated with high O2 concentration than with lower salinity. Nevertheless: loss of pleopod setation is clearly a character evolved under selection pressure in the hypogean aquatic environment of low(er) salinity, and can be associated, at least in many cases, with reduction or loss of the natatory ability of the pleopods.

In a few stygobitic species there is a degree of general rudimentation of the pleopods, not equalled in any marine species. *Faucheria faucheri* has very small and polymorphic pleopods covering only 1/2 of the sternal face of the pleotelson, the rami of Pl. I-II being reduced to narrow chitinous straps; *Faucheria* is definitely unable to use such pleopods for swimming (Racovitza 1912).

Finally, 5 stygobitic species in 4 different genera share a remarkable character never present in any marine cirolanid: deeply split (bilobed), endopodites of Pl. III-V. It was a regrettable error of mine to state in the original description of *Jamaicalana pleoscissa* Botosaneanu & Iliffe, 1997, that this character is uniquely present in this species. In Fig. 27 only Pl. V is illustrated for *Cirolana (Anopsilana) pleoscissa, Skotobaena monodi, Zulialana coalescens,* and *Sphaeromides raymondi* Dollfus, 1897; but the situation is similar for Pl. III-IV (also *Skotobaena mortoni* has similarly split endopodites). We have here at the same time rudimentation *and* novelty clearly associated with subterranean life. Despite slight differences in morphological detail, the significance of such a structure is likely fundamentally the same in all these species: maybe either enhancement (in rela-

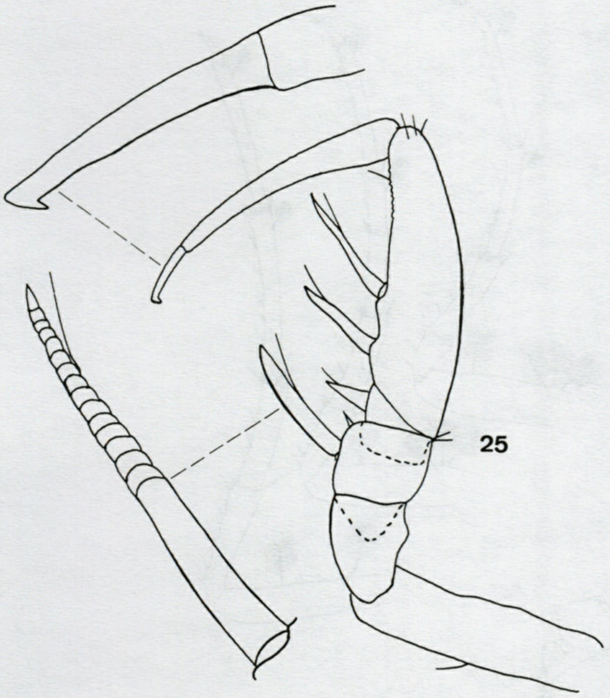


Fig. 25. – *Yucatalana robustispina* Botosaneanu & Iliffe, 1999, left PI, with one of the huge spines and the unguis more strongly magnified (from the original description).

tion with transition from marine water to lower ionic concentrations), or lowering (in relation with metabolic economy) of O2 consumption. But its significance could be different: according to Wägele (1992: 564) the pleopod endopodites are mainly involved in osmoregulation, in contrast with the respiratory exopodites. Anyway, I am tempted to consider such situations as being diametrically opposed to that found in species of the small marine genera *Bathynomus* and *Parabathynomus,* with their "grapes" of gills on all pleopod endopodites (*B.*) or coxopodites (*P.*).

Some particular structures in hypogean species

In *Sphaeromides polateni* Angelov, 1968, a troglostygobiont from Bulgaria, AII are sexually dimorphic, the last peduncular article in the ♂ (Fig. 24) being not only strongly widened, but also twisted, in a manner helping the male to take hold of the Ist pereional epimera of the female during mating (Angelov 1968: 212). It is possible that the sexual dimorphism described for the propodus of PIII of *Typhlocirolana margalefi* (Pretus, 1986: 100, fig. 5) is a similar case. Is there some relation between hypogean life and such structures ? It is possible that a structure efficient in holding mates has its selective value in the special conditions characterizing the hypogean environment.

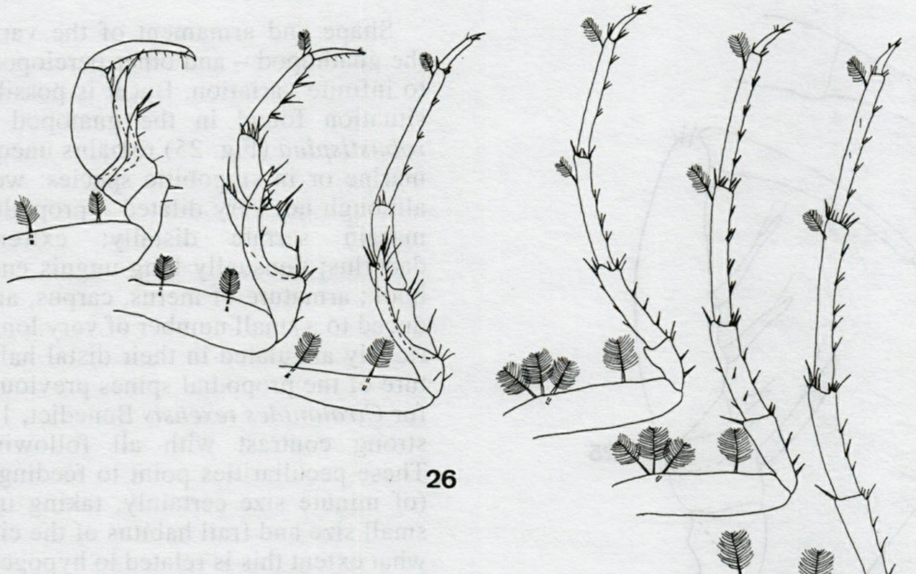
Shape and armament of the various articles of the gnathopod – and other pereiopods – are subject to infinite variation. But it is possible that the odd situation found in the gnatopod of *Yucatalana robustispina* (Fig. 25) remains unequalled either in marine or in stygobitic species: well developed – although not very dilated – propodus, with palmar margin serrate distally; extremely elongate dactylus; unusually long unguis ending in a small hook; armature of merus, carpus, and propodus reduced to a small number of very long spines, all curiously annulated in their distal half (such a structure of the propodial spines previously known only for *Cirolanides texensis* Benedict, 1896); all this in strong contrast with all following pereiopods. These peculiarities point to feeding on living prey (of minute size certainly, taking into account the small size and frail habitus of the cirolanid). But to what extent this is related to hypogean life, remains unanswered.

Bowman (1992) describes in *Cirolanides texensis* a "precocious gnathopod development". His illustration (here reproduced: Fig. 30) shows, to the same scale, the gnathopod in a 5.7 mm juvenile, and a 13 mm adult ♂, from the same sample, the conclusion being that the juvenile propodus has grown allometrically at nearly twice the rate of the body, and that clear differences between the two are seen in the shape of the propodial palm and in the length of the dactylus, all this suggesting "a need for the juvenile to handle objects that a gnathopod developing isometrically could not cope with". A similar situation has not been described for another cirolanid.

Generally speaking, sexual dimorphism in Cirolanidae is described as slight, if not practically absent (of course, if abstraction is made of the modified Pl. II and the presence of penes/genital papillae in the ♂♂, or of oostegites and of modified maxillipeds in ♀♀ with oostegites). In a few marine species (in the genera *Booralana, Limicolana, Metacirolana...*), or in the species of *Annina,* some of them to some extent stygophile, a rather strong sexual dimorphism is present (see, i.a., discussion in Bowman & Iliffe 1991). Nevertheless, I believe that nowhere in the family is the sexual dimorphism so conspicuous as that displayed by the uropods of 3 related species of the stygobitic genus *Speocirolana*: *S. lapenita* Botosaneanu & Iliffe, 1999 (Fig. 28), *S. pubens* Bowman, 1981 (Fig. 29), and probably also *S. guerrai* Contreras-Balderas & Purata-Velarde, 1981 – all from Mexico.

The propodial organs

Racovitza (1912: 238-241, 246) gave the first description of curious organs discovered on the propodus of pereiopods II and III in both sexes of



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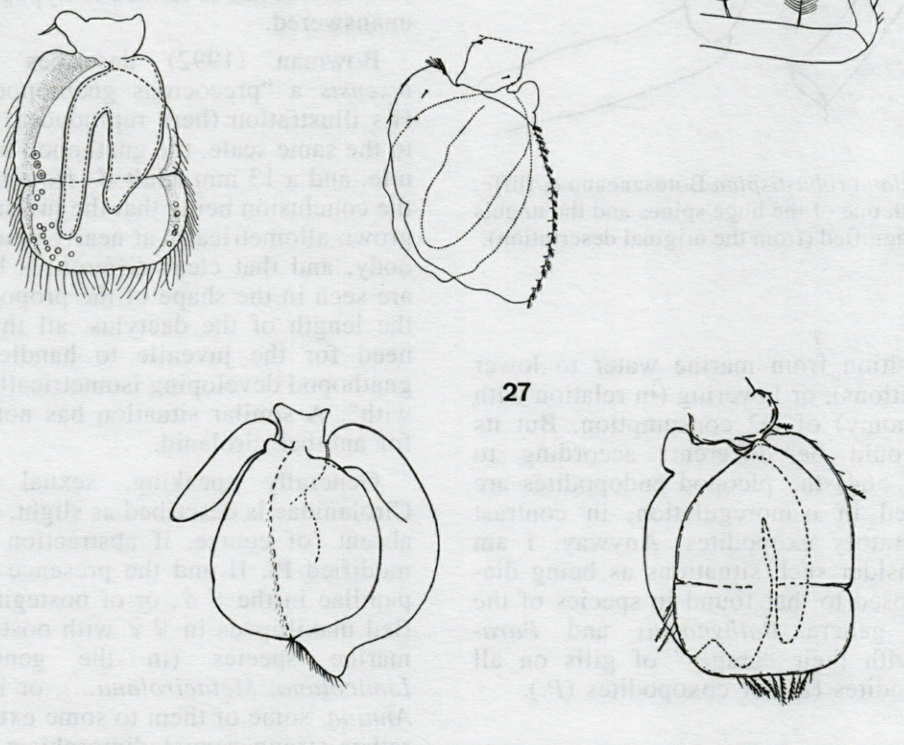

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Fig. 26. – *Bahalana yagerae* (Carpenter, 1994), left pereiopods of a mature male (from the original description). – Fig. 27. – Pleopod V of *Cirolana (Anopsilana) pleoscissa* (Botosaneanu & Iliffe, 1997) (above, left), *Skotobaena monodi* Ferrara & Lanza, 1968 (above, right), *Zulialana coalescens* Botosaneanu & Viloria, 1993 (below, left), and *Sphaeromides raymondi* Dollfus, 1897 (below, right); first three from the original publications, last one from Racovitza 1912.

Typhlocirolana moraguesi Racovitza, 1905; he coined for them the term "propodial organs" and offered a detailed discussion on their structure and possible significance. These organs are rather large round or elliptical "blades" externally placed on the anterior surface of the propodus; separated from its cuticula by a thin membrane, they are relatively easily detached (which could explain their absence in some examined specimens). Their surface looks like a honeycomb, but the cells of this honeycomb are, in fact, complex organites described in detail by Racovitza by means of sections (Fig. 21 shows a sectioned propodial organ, and a detail with a few organites); he describes the organ surface as being covered by truncate hexagonal pyramids, on each pyramid an externally concave disk being placed. The propodial organs –of a type never described in other crustaceans or arthropods– are tentatively considered by Racovitza as being adhesive organs, the "disks" maybe acting as suckers. To this day, no other explanation for their function has been proposed; apparently not having

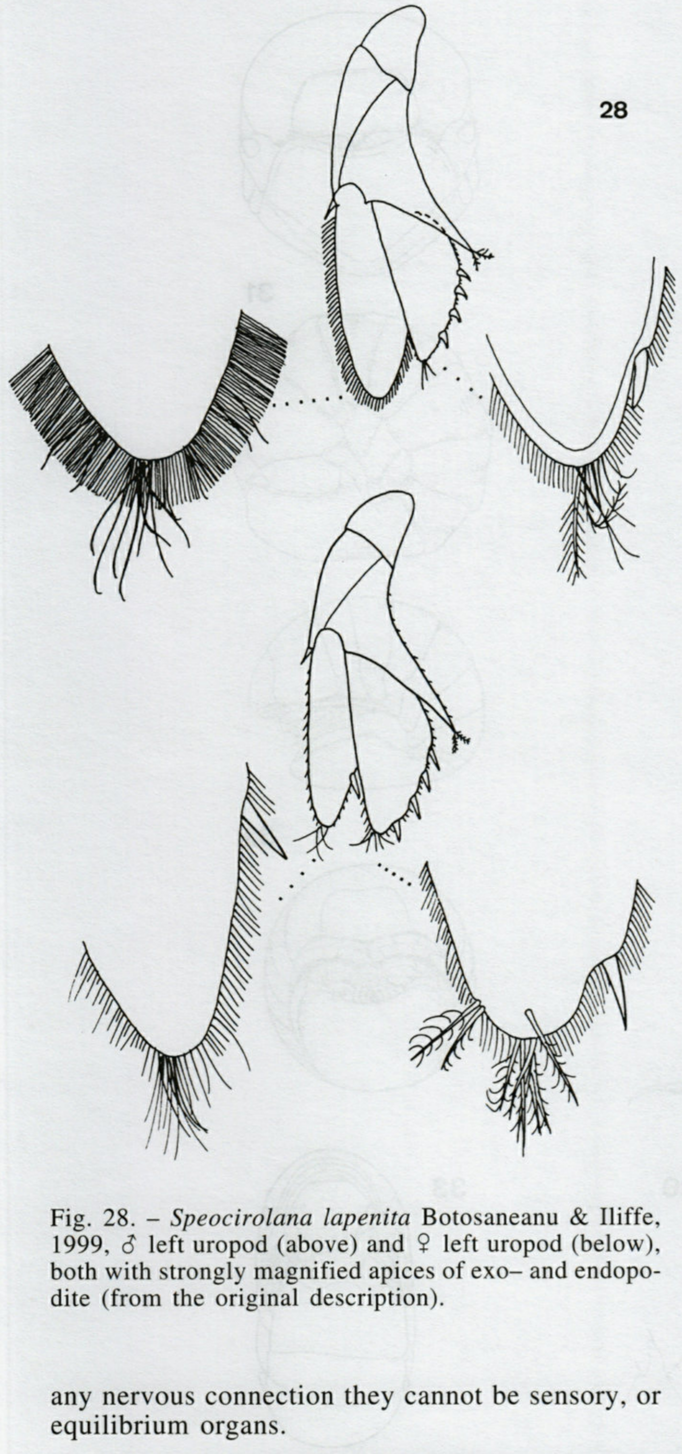


Fig. 28. – *Speocirolana lapenita* Botosaneanu & Iliffe, 1999, ♂ left uropod (above) and ♀ left uropod (below), both with strongly magnified apices of exo– and endopodite (from the original description).

any nervous connection they cannot be sensory, or equilibrium organs.

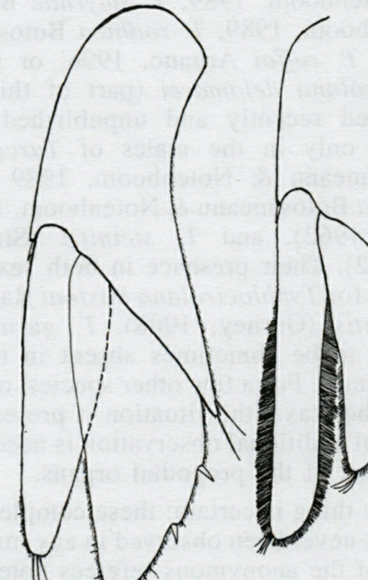
Subsequently, propodial organs were mentioned and sometimes illustrated for adults of several species in the closely related genera *Typhlocirolana* and *Turcolana.* The situation is complex, because in some species they were not found, whereas in others they are present in both sexes, or only in the males, but always on the propodus of P II and P III (although – Nourisson 1956 – such an organ was found only on P III in a ♂ of *Typhlocirolana gurneyi* Racovitza, 1912). Propodial organs were not found in *Typhlocirolana leptura*, *T. margalefi* Pretus, 1986, *Turcolana pamphyliae* Botosaneanu & Notenboom, 1989, *T. smyrnae* Botosaneanu & Notenboom, 1989, *T. rodhica* Botosaneanu *et al.*, 1985, *T. ruffoi* Argano, 1996, or in the related *Marocolana delamarei* (part of this information obtained recently and unpublished). They were found only in the males of *Turcolana adaliae* Botosaneanu & Notenboom, 1989 (Fig. 23), *T. detecta* Botosaneanu & Notenboom, 1992, *T. reichi* (Por, 1962), and *T. steinitzi* (Strouhal, 1960; Fig. 22). Their presence in both sexes was ascertained for *Typhlocirolana buxtoni* Racovitza, 1912, *T. fontis* (Gurney, 1908), *T. gurneyi* (where it seems to be sometimes absent in the ♀, and *T. moraguesi*. For a few other species, or not formally described taxa, the situation is presently unsettled. Careful additional observation is needed on the distribution of the propodial organs.

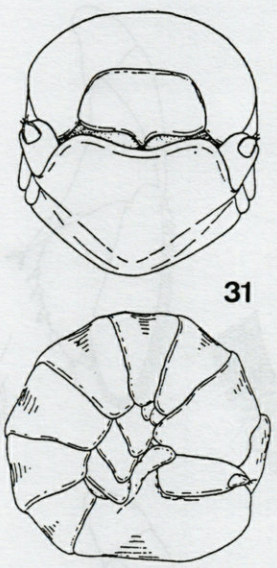
One thing is certain: these complex organs have almost never been observed in any marine cirolanid (one of the anonymous referees notes the interesting fact that such organs were discovered in the genus *Colopisthus* Richardson (paper in press); and it would be absurd to believe that several generations of carcinologists have failed to observe them. They are thus a remarkable novelty in a phyletic line entirely subterranean-adapted of the family, this contradicting an idea expressed by Racovitza (1912: 247): [the propodial organs] "... ne semblent pas pouvoir être attribués à la vie souterraine; ils devaient caractériser la lignée avant la colonisation souterraine".

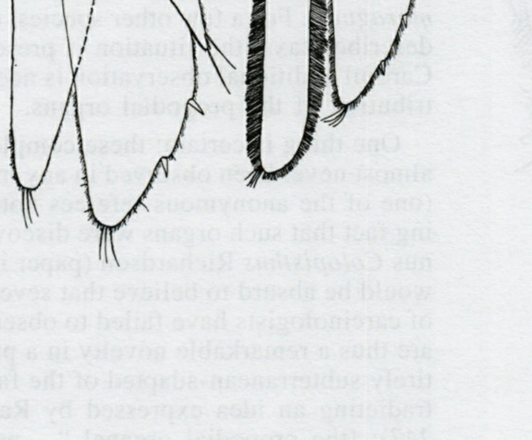
Volvation

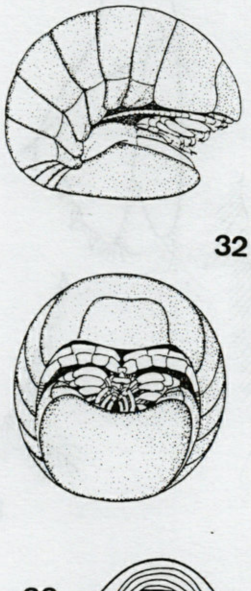
The ability of rolling the body more or less completely into a ball is known in several groups of Arthropods; in Isopoda it is observed in several widely distant groups, being in some of them a very frequent phenomenon (for instance in the aquatic suborder Sphaeromatidea, or in various terrestrial taxa, groups for which excellent studies have been published on the volvational mechanism and the morphological implications of volvation). Various explanations of its utility have been offered, the most plausible – and supported by some published information – being that it is the result of a defense reflex enabling animals to avoid being grasped by potential predators and protect the tender ventral parts of the body with their appendages, as well as the brood.

It is significant that, whereas no case of volvation, even incipient, is known in marine Cirolanidae, several such cases are known in phylogenetically widely distant subterranean species, this being evidence that "Il se peut que l'enroulement soit acquis après la colonisation souterraine sous l'influence de la lutte pour l'existence" (Racovitza 1912), that "... la volvation a pu se voir acquise en rapport avec la vie









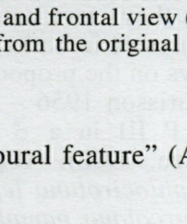


Fig. 29. – *Speocirolana pubens* Bowman, 1981, uropod of ♀ (left) and of ♂ (right) (from the original description). – Fig. 30. – *Cirolanides texensis* Benedict, 1896, right PI of a mature ♂ (left) and of a juvenile (right) (from Bowman, 1992). – Fig. 31. – *Faucheria faucheri* (Dollfus & Viré, 1900), ♀ rolled into a ball, frontal and lateral view (from Racovitza 1912). – Fig. 32. – *Skotobaena mortoni* Monod, 1972, rolled into a ball, lateral and frontal view (from the original description). – Fig. 33. – *Marocolana delamarei* Boutin, 1993, rolled into a ball (from the original description).

endogée" (Monod 1972), and of "... the existence, in the subterranean aquatic environments, of ecological conditions favourable to the adaptive success of this behavioural feature" (Argano & Pesce 1980).

Not all cases of volvational ability in stygobitic cirolanids are described with enough detail, and in some cases uncertainty reigns about the degree to which volvation is achieved. Volvation can be "perfect" or "almost perfect" in *Creaseriella anops* (Creaser, 1936); *Faucheria faucheri* (Fig. 31; detailed description of morphological implications, and considerations about "origine de l'enroulement": Racovitza 1912); and *Zulialana coalescens* (observations on morphological implications, and field and aquarium observations on the volvational behaviour: Botosaneanu & Viloria 1993). In *Marocolana delamarei* (Fig. 33) the volvation observed on living animals is described as complete (Boulanouar *et al.* 1993) – but it is possibly imperfect. Despite the genus name and a short note in the original description, the situation in *Sphaerolana* is not clear: in specimens of *S. interstitialis* and *S. affinis* kept in alcohol, I have observed only a slight tendency to volvation; moreover, in Cole & Minckley (1970) we find that in a mixed population of these two species, the 2nd one "appeared unable to roll tightly when disturbed". "Imperfect" volvation, but with specific differences inside a genus, was reported for *Skotobaena* (Fig. 32; discussion on morphological implications and on behaviour: Monod 1972); and for *Turcolana* (especially discussion, partly based on observations on living animals, in Botosaneanu & Notenboom 1989; for some species ability to roll completely into a ball was reported, but this is contradicted by published illustration and should be taken with caution).

Several observations were made on volvation as a direct reaction to disturbance by coexisting animals, or by man. And it is quite plausible that in a cave pool the impact of mighty, turbulent animals like crustaceans or fishes on blind and sensitive cirolanids may be stronger than in the open sea. Finally, that volvation may act as protection against dessication, was observed in *Zulialana coalescens* (Botosaneanu & Viloria, 1993); taking into account the fact, several times noticed, that cave cirolanids have the habit of leaving their aquatic environment for roaming in its vicinity, this is possibly a rather frequently acting survival strategy.

Paedomorphy in Bahalana yagerae

A situation unique for Cirolanidae (although known in several other isopod groups: Gnathiidae, Protognathiidae, a few Anthuridae, some deep sea Asellota) was described by Carpenter (1994) for *Dodecalana yagerae*, a species inhabiting fully marine caves on Grand Bahama Island: the existence of only 6 pairs of pereiopods in all mature males and females caught. The fact that P III-VI (Fig. 26) in this species are all longer than any pereiopods in specimens of the same size of the closely related *Bahalana geracei*, could be, according to Carpenter, an adaptation to compensate for the instability accompanying loss of P VII. This is a case of paedomorphy: is there a direct relation between it and hypogean life ? Not necessarily, but to all appearances there is one. It should be added that in the marine genus *Seychellana*, PVII is strongly reduced.

Facts related to "K-strategy"

K-Selection implies, i.a.: reduced reproductive effort, low number of offspring, and delayed maturity. For various groups of stygobitic animals there is at present abundant evidence of low reproductive rates (few but large, yolky eggs produced; reduced populations) and increased longevity (heterogeneity in age class structure of the populations), all this in contrast with the situation in related epigean taxa. The rather scarce, and not always rigorous evidence for Cirolanidae, does not contradict this pattern.

In the marsupium of a ♀ of *Yucatalana robustispina* only 3 very large eggs were found (Botosaneanu & Iliffe 1999) but that of another specimen was filled with 10 large pulli. A single pullus was found in the marsupium of a ♀ of *Skotobaena mortoni,* and this "laisse à penser que le nombre des œufs par ponte est très réduit et peut-être même limité à un seul" (Monod 1972). In the marsupium of a specimen of *Cirolanides texensis* ssp. *mexicensis* Botosaneanu & Iliffe, 2001, I have found 10 big eggs. There are several observations on species of the *Typhlocirolana-Turcolana* lineage; despite inconsistency of terminology used in various publications, one apparently interesting pattern emerges: eggs (?), if present, are found in *the general cavity*, oostegites having never been observed in this group. In 3 ♀ of *Turcolana reichi* "ovaires jaunes et pleins d'œufs immatures" were observed (Por 1962). In *T. rodhica* ♀ was found "à ovocytes mûrs visibles dorsalement par transparence" (Botosaneanu *et al. 1985; "ovocytes" is, possibly, an error). The* ♀ allotype of *T. pamphyliae* was described and illustrated (Botosaneanu and Notenboom 1989) as having "two large eggs... inside the 6th pereional segment". And Racovitza (1912) describes 1 ♀ of *Typhlocirolana gurneyi* as having one dozen eggs in the general cavity – which would be a record for stygobitic Cirolanidae, should this observations be confirmed. All this is evidence for internal brooding of eggs in *Typhlocirolana-Turcolana* (ovovivipary is recorded for very few epigean – marine or from continental water – cirolanids, as well as for the epigean and slightly stygophilic, fresh/brackish water *Annina lacustris*). This evidence should be compared with the situation found in some epigean – mostly marine – Cirolanidae. *Annina mesopotamica* (Ahmed, 1971): "mean 24 eggs" (Salman, Oshana & Ali 1996); *Bathynomus giganteus* Milne Edwards, 1879: 26 eggs (Lloyd 1908); *Cirolana harfordi* (Lockington, 1877): 18-68 eggs per brood (Johnson 1976); *Eurydice pulchra* Leach, 1815 and *E. affinis* Hansen, 1905: 30-45 and, respectively, 18-29 eggs (Jones 1970); *Excirolana braziliensis* Richardson, 1912: 10-27 "embryoes" or "huevos" (Zuñiga *et al.* 1985); "Number of eggs per brood ranged from 4 to 17 (Dexter 1977); *Excirolana chiltoni* (Richardson 1905): "average 30.7 eggs (Klapow 1970); *Natatolana borealis* (Lilljeborg, 1851): "The number of eggs, embryos and larvae found in the marsupia varied from 23 to 77, averaging 50.9" (Johansen 1996); *Pseudolana concinna* (Hale, 1925): mean 13.29 and mean 27.80 eggs in two different populations (Dexter 1985); *P. towrae* Bruce, 1983: 18-24 eggs (Dexter 1985).

In numerous subterranean cirolanid species conspicuous intrapopulational differences in size of mature specimens were noticed. In a populational study of *Antrolana lira* Bowman, 1964, adults in two populations measured between 9 and 21 mm (Collins & Holsinger 1981). In a population of *Speocirolana pelaezi* (Bolivar y Pieltain, 1950) mature females measuring between 8.5 and 31 mm were found (Botosaneanu & Iliffe 1999). Dwarf mature specimens as small as 5 mm and as 3 mm were found by Carpenter (1981) in the otherwise large *Bahalana geracei* and, respectively, *B. mayana*; the same author found, in many months of laboratory observation on *B. geracei*, only one moulting specimen. *Jamaicalana pleoscissa* was described from a ♀ specimen measuring 10 mm, the only other specimen being a fully developed dwarf ♀ of only 3.6 mm.

DISCUSSION

How to explain the fascinating diversity of morphological and other adaptive responses of stygobitic Cirolanidae ? Ideas formulated by Danielopol & Rouch (1991) could be summarized as follows.

1. *The subterranean aquatic environment is more complex than considered in traditional biospeology*. This seems to be true in the light of recent research. From the three main factors recognized as essential in classical biospeology (complete darkness, scarcity of trophic resources, environmental constancy), the first one is indisputably of paramount importance. Concerning the 2d one, it is presently evident that, if oligotrophy is often – but certainly not always – one element of the trophic factor, others should be equally well taken into consideration: sources, quality, patchiness, seasonal variation of available trophic resources; moreover, an aspect which could prove to be of some importance: the feeding modes (trophic categories) of the members of an assemblage of hypogean living species. And a specification is indispensable concerning the 3d factor: indeed, quite frequently the habitats of subterranean Cirolanidae, especially in karstic environments and even more so in tropical ones, are characterized by an extremely unstable hydrological regime (water depth and flow, current speed, turbidity...), or chemical regime (salinity stratification and fluctuations in anchialine or other near-shore environments...). All this represents quite serious constraints of the rigorous subterranean habitats.

2. *Animals display a great variety of adaptive responses to this environment/there is a positive relationship between subterranean habitat diversity and these adaptive responses.* This idea is well supported by evidence presented in this paper.

The answer for some of the questions asked in the present paper will be found by more thorough study of the trophic factor (see above) and of the biocenotic factors (exact composition of the biocenoses, population densities, interspecific relations).

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A SYNOPTIC KEY TO THE RHODOPHYTA OF THE WESTERN MEDITERRANEAN PART. I GIGARTINALES, HALYMENIALES, HILDENBRANDIALES AND PLOCAMIALES

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RHODOPHYTES
GIGARTINALES
HALYMENIALES
HILDENBRANDIALES
PLOCAMIALES
CLÉ TAXONOMIQUE
STRUCTURES DE REPRODUCTION
MÉDITERRANÉE DE L'OUEST

RÉSUMÉ. – Une clé dichotomique pour la détermination des Gigartinales, Halyméniales, Hildenbrandiales et Plocamiales de Méditerranée occidentale est présentée. Elle a pour objectif de faciliter la reconnaissance de ces algues rouges. Ce travail inclut l'ordre des Gigartinales, avec 69 espèces groupées en 19 familles et 35 genres, l'ordre des Halyméniales, avec 13 espèces appartenant à 2 familles et 6 genres, l'ordre des Hildenbrandiales, avec 1 famille, 1 genre et 3 espèces, et l'ordre des Plocamiales, avec 1 famille, 1 genre et 2 espèces. Le genre *Wurdermannia* Harvey est inclus dans la clé, bien que son appartenance aux Gigartinales reste incertaine. Quelques descriptions morphologiques et anatomiques des structures de reproduction sont aussi incluses, d'après des données de la littérature et de nos propres observations.

RHODOPHYTA
GIGARTINALES
HALYMENIALES
HILDENBRANDIALES
PLOCAMIALES
TAXONOMIC KEY
REPRODUCTIVE STRUCTURES
WESTERN MEDITERRANEAN

ABSTRACT. – A synoptic key for identifying the Gigartinales, Halymeniales, Hildenbrandiales and Plocamiales from the Western Mediterranean has been prepared in order to facilitate the recognition of these red algae. The orders Gigartinales, with some 69 species grouped in 19 families and 35 genera, Halymeniales, with 13 species grouped in 2 families and 6 genera, Hildenbrandiales, with 1 family and 1 genera of 3 species, and Plocamiales, with 1 family and 1 genus of 2 species are included. The genus *Wurdermannia* Harvey is also included in the key, although it has not finally been established whether it belongs to the order Gigartinales or not. Morphological and anatomical descriptions of the reproductive structures, using data from the literature and from personal observations are presented.

INTRODUCTION

This is intended to be the first publication in a series of keys to the different orders of benthic marine algal flora from the western Mediterranean (excluding the recently introduced species). The present paper includes the order Gigartinales with 69 species grouped in 19 families and 35 genera, the order Halymeniales with 13 species grouped in two families and six genera, the order Hildenbrandiales with one family and one genus of three species, and the order Plocamiales, with one family and one genus of two species. The genus *Wurdermannia* Harvey is also included in the key although it has not yet been finally established whether it belongs to the order Gigartinales or not.

The key should serve as a tool to identify genera and species of these groups. An effort has been made to base dichotomies in the key upon more than a single distinction. Vegetative characteristics are used to separate genera and species where appropriate, but as definitive identification can only rarely be obtained from general appearance and form of the Rhodophyta, or from sterile material, reproductive stages have been incorporated in unavoidable cases. Many of the families have a highly distinctive female reproductive system from which they can be recognized, although such characters may often be difficult to observe. The main reproductive characteristics are listed for each genus in Table I. The use of dimensions such as the length and width of thalli is only a guide in the key, since such characteristics tend to be very variable and unstable.

Following the key is a listing of the genera and species currently recognized in the studied area. We have included the order Cryptonemiales (Kylin, 1956) in the order Gigartinales, following Kraft & Robins (1985), because we consider that

ORDER	**GIGARTINALES**														
FAMILY	Acrosymphytaceae	Calosiphoniaceae		Caulacanthaceae			Cruoriaceae	Cystocloniaceae		Dumontiaceae	Furcellariaceae		Gigartinaceae	Gloiosiphoniaceae	
GENUS	*Acrosymphyton*	*Calosiphonia*	*Schmitzia*	*Catenella*	*Caulacanthus*	*Feldmannophycus*	*Cruoria*	*Calliblepharis*	*Rhodophyllis*	*Dudresnaya*	*Halarachnion*	*Neurocaulon*	*Chondracanthus*	*Gloiosiphonia*	*Thuretella*
structure Uniaxial/Multiaxial	U	U	U	U	U	U	▨	U	U	U	M	M	M	U	U
LIFE HISTORY															
Triphasic/Biphasic	T	T	?	T	T	T	T	T	T	T	T	T	T	T	?
Isomorphic/Heteromorphic	H	H	?	I	I	I	I	I	I	I/H	H	H	I	H	?
FEMALE GAMETANGIA															
Monocarpogonial/Polycarpogonial	M	M	M	M	M	M	M	M	M	M	M	M*	M	M/P	M
number of cells of the carpogonial branch	sv	3	3	2-5	3	2-5	2-3	3	3	sv	3	3	3	3	3
carpogonial branch Simple/Branched	B	S	S	B*	S	S	S	S	S	S*	S	S	S	S	S
Procarpic/Non-procarpic	N	N	N	N	N	N	?	P	P	N	N	N	P	P	P
supporting cell acting as auxiliary cells (Yes/No)	▨	▨	▨	▨	▨	▨	?	N	N	▨	▨	▨	Y	N	N
auxiliary branch borne on supporting cell (Yes)	▨	▨	▨	▨	▨	▨	?	Y	Y	▨	▨	▨	▨	Y	Y
auxiliary cell a nearby cortical or medullar cell (Yes)	▨	Y	Y	Y	Y	Y	?	▨	▨	▨	Y	Y	▨	▨	▨
auxiliary cells in special filaments (Yes)	Y	▨	▨	▨	▨	▨	?	▨	▨	Y	▨	▨	▨	▨	▨
carpogonial and auxiliary cells in ampullae	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
subsidiary cells present (Yes)	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
carpogonial branch with nutritive auxiliary cells (Yes)	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
auxiliary cell with adjacent nutritive cells (Yes)	Y	▨	▨	▨	▨	▨	▨	Y	Y	Y	▨	▨	▨	▨	▨
MALE GAMETANGIA															
Scattered/in Clusters/in SOri/in CHains	C	C	C	S	S	C	SO	S	S	C	SO	SO	SO	C	C
in special branchlets or bladelets (Yes/No)	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N
GONIMOBLAST															
developing Inwards/Outwards	O	O	O	I	I	I	?	I	?	O	I	?	I	O	O
on Auxiliary cell/on Connecting filament	C	A	C	A	A	A	?	▨	▨	C	A	?	▨	▨	▨
with involucre Cellular/Filamentous/Absent	A	A	A	A	A	A	?	C	C	A	A	A	C	A	A
with ostiole Present/Absent	A	A	A	P*	P*	P*	A	A	A*	A	P	A	A	A	A
in special branchlets or bladelets (Yes/No)	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N
TETRASPORANGIA															
Cruciately/Tetrahedrally/Zonately/Irregularly arranged	T/Z	C	?	Z	Z	Z	Z	Z	Z	Z*/C	Z	Z	C	C	?
Scattered/in SOri/in Conceptacles	S	?	S	S	S	SO	S	S	S	S	S	?	S	S	?
in special branchlets or bladelets (Yes/No)	N	N	N	N	N	N	N	Y*	Y*	N	N	N	N	N	?

ORDER	**GIGARTINALES**														
FAMILY	Gloiosiphoniaceae	Hypneaceae	Kallymeniaceae			Nemastomataceae		Peyssonneliaceae			Phyllophoraceae			Rhizophyllidaceae	Rissoëllaceae
GENUS	*Schimmelmannia*	*Hypnea*	*Callophyllis*	*Kallymenia*	*Meredithia*	*Nemastoma*	*Predaea*	*Metapeyssonnelia*	*Peyssonnelia*	*Polystrata*	*Gymnogongrus*	*Phyllophora*	*Schottera*	*Contarinia*	*Rissoëlla*
structure Uniaxial/Multiaxial	U	U	M	M	M	M	M	▨	▨	▨	M	M	M	▨	M
LIFE HISTORY															
Triphasic/Biphasic	?	T	T	T	T	T	T	?	T	?	B	T	T	T	T
Isomorphic/Heteromorphic	?	I	I	I	H	H	H	?	I	?	H	I	I	I	I
FEMALE GAMETANGIA															
Monocarpogonial/Polycarpogonial	M	M	M/P	M/P	M/P	M	M	?	M	?	M	M	M	?	M
number of cells of the carpogonial branch	4	3*	2	2	2	3	2-5	?	3-6	?	2/4	3-4	4	?	2-3
carpogonial branch Simple/Branched	B	S	S	S	S	S	S	?	S	?	B	S	S	?	S*
Procarpic/Non-procarpic	P	P	P	N	N	N	N	?	N	?	P	P	P	?	P
supporting cell acting as auxiliary cells (Yes/No)	N	N	Y	▨	▨	▨	▨	?	▨	?	Y	Y	Y	?	Y
auxiliary branch borne on supporting cell (Yes)	Y	Y	▨	▨	▨	▨	▨	?	▨	?	▨	▨	▨	?	▨
auxiliary cell a nearby cortical or medullar cell (Yes)	▨	▨	▨	▨	▨	Y	Y	?	▨	?	▨	▨	▨	?	▨
auxiliary cells in special filaments (Yes)	▨	▨	▨	Y	Y	▨	▨	?	Y	?	▨	▨	▨	?	▨
carpogonial and auxiliary cells in ampullae	▨	▨	▨	▨	▨	▨	▨	?	▨	?	▨	▨	▨	?	▨
subsidiary cells present (Yes)	▨	▨	Y	Y	Y	▨	▨	?	▨	?	▨	▨	▨	?	▨
carpogonial branch with nutritive auxiliary cells (Yes)	▨	▨	▨	▨	▨	▨	▨	?	▨	?	▨	▨	▨	?	▨
auxiliary cell with adjacent nutritive cells (Yes)	▨	Y	▨	▨	▨	▨	Y	?	▨	?	▨	▨	▨	?	▨
MALE GAMETANGIA															
Scattered/in Clusters/in SOri/in CHains	C	CH	SO	S	S	C	C	?	SO	?	SO	SO	SO	SO	SO
in special branchlets or bladelets (Yes/No)	N	Y	N	N	N	N	N	?	N	?	N	N	N	N	N
GONIMOBLAST															
developing Inwards/Outwards	O	I	I/O	O	O	O	O	?	O	?	I	I	I	?	I
on Auxiliary cell/on Connecting filament	▨	▨	▨	C*	?	C	C/A	?	C	?	▨	▨	▨	?	▨
with involucre Cellular/Filamentous/Absent	A	C	F	A	A	A	A	?	A	?	▨	C	C	?	?
with ostiole Present/Absent	A	A	P	P/A	A	P	P*	?	A	?	▨	A	A	A	P
in special branchlets or bladelets (Yes/No)	N	N	Y/N	N	N	N	N	?	N	?	N	Y	N	N	N
TETRASPORANGIA															
Cruciately/Tetrahedrally/Zonately/Irregularly arranged	?	Z	C	C/Z	Z	?	C/Z	?	C	C	C	C	C	C/Z/I	Z
Scattered/in SOri/in Conceptacles	?	SO	S	S	S	?	S	?	SO	SO	SO	SO	SO	SO	S
in special branchlets or bladelets (Yes/No)	?	Y	Y*	N	N	?	N	?	N	N	N	N	N	N	N

ORDER	**GIGARTINALES**				**HALYMENIALES**						HILDENBRANDIALES	PLOCAMIALES	?
FAMILY	Sarcodiaceae	Schizymeniaceae		Sphaerococcaceae	Halymeniaceae					Sebdeniaceae	Hildenbrandiaceae	Plocamiaceae	*Incertae sedis*
GENUS	*Chondrymenia*	*Platoma*	*Schizymenia*	*Sphaerococcus*	*Acrodiscus*	*Aeodes*	*Cryptonemia*	*Grateloupia*	*Halymenia*	*Sebdenia*	*Hildenbrandia*	*Plocamium*	*Wurdemannia*
structure Uniaxial/Multiaxial	M	M	M	U	M	M	M	M	M	M	▨	U	M
LIFE HISTORY													
Triphasic/Biphasic	?	T	T	T	?	T	T	T	T	T	▨	T	?
Isomorphic/Heteromorphic	?	H	H	I	?	I	I	I	I	I	▨	I	?
FEMALE GAMETANGIA													
Monocarpogonial/Polycarpogonial	?	M	M	M	?	M*	M	M	M/P	M	▨	M	?
number of cells of the carpogonial branch	?	3	3	3	?	2	2	2	2	2-4	▨	3	?
carpogonial branch Simple/Branched	?	S	S	S	?	S	S	S	S	S	▨	S	?
Procarpic/Non-procarpic	?	N	N	P	?	N	N	N	N	N	▨	P	?
supporting cell acting as auxiliary cells (Yes/No)	?	▨	▨	Y	?	▨	▨	▨	▨	▨	▨	Y	?
auxiliary branch borne on supporting cell (Yes)	?	▨	▨	▨	?	▨	▨	▨	▨	▨	▨	▨	?
auxiliary cell a nearby cortical or medullar cell (Yes)	?	Y	Y	▨	?	▨	▨	▨	▨	Y	▨	▨	?
auxiliary cells in special filaments (Yes)	?	▨	▨	▨	?	Y	Y	Y	Y	▨	▨	▨	?
carpogonial and auxiliary cells in ampullae	?	▨	▨	▨	?	Y	Y	Y	Y	▨	▨	▨	?
subsidiary cells present (Yes)	?	▨	▨	▨	?	▨	▨	▨	▨	▨	▨	▨	?
carpogonial branch with nutritive auxiliary cells (Yes)	?	Y	Y	▨	?	▨	▨	▨	▨	▨	▨	▨	?
auxiliary cell with adjacent nutritive cells (Yes)	?	▨	▨	▨	?	▨	▨	▨	▨	Y	▨	Y	?
MALE GAMETANGIA													
Scattered/in Clusters/in SOri/in CHains	?	C	C	SO	?	S	S	S/S	SO	S/SO	▨	SO	?
in special branchlets or bladelets (Yes/No)	?	N	N	N	?	N	N	N	N	N	▨	N	?
GONIMOBLAST													
developing Inwards/Outwards	O	O	O	O	?	?	O	O	I	O	▨	O	?
on Auxiliary cell/on Connecting filament	?	A	A	▨	?	A	A	A	A	A	▨	▨	?
with involucre Cellular/Filamentous/Absent	?	A	F	C	?	F	F	F	F	F	▨	C	?
with ostiole Present/Absent	P	P	P	A	?	A	P	P	P	P	▨	A	?
in special branchlets or bladelets (Yes/No)	N	N	N	Y	?	N	Y*	N	N	N	▨	Y*	?
TETRASPORANGIA													
Cruciately/Tetrahedrally/Zonately/Irregularly arranged	?	?	Z/C	Z	C	C	C	C	C	C/I	Z	Z	Z
Scattered/in SOri/in Conceptacles	?	?	S	SO	SO	S	S	S	S	S	C	SO	SO
in special branchlets or bladelets (Yes/No)	?	N	N	N	N	N	N*	Y*	N	N	N	Y	N

Table 1. Type of structure and main reproductive characteristics of the genera treated (sv = several); (* = usually); (? = unknown); (grey colour = unattainable characteristics).

the fact that the Cryptonemiales have auxiliary cells in accessory systems within the thallus, as opposed to Gigartinales supposedly transforming vegetative cells into auxiliary cells, is insufficient basis for placing the Cryptonemiales in a separate order. The Hildenbrandiales (Pueschel & Cole, 1982), Plocamiales (Saunders & Kraft, 1994) and Halymeniales (Saunders & Kraft, 1996) are considered as separate orders, following recent molecular studies, but since their morphology and reproductive structures are similar to the Gigartinales, the families in these orders are not separated in the key. Other taxa have been separated as orders and are not covered in this first part. These taxa included the Ahnfeltiales (Maggs & Pueschel, 1989), representatives of which are not known in Western Mediterranean, the Corallinales (Silva & Johansen, 1986), which is a clearly distinguishable order, and the Gracilariales (Fredericq & Hommersand, 1989) which requires more investigation in the Mediterranean. The taxonomic arrangement below the level of families follows Silva *et al.* (1996).

CURRENT KEY

1. Thallus prostrate, with a dorsiventral symmetry. Plants calcified or not. Structure consisting of a single basal layer of branched filaments (hypothallus), with each cell dividing into one or more upper cells (upper *coxal* cells) and, occasionally, one or more lower cells (lower *coxal* cells). The upper *coxal* cells give rise to filaments of apical growth directed to the upper surface (perithallus), erect or slightly inclined towards the margin. In the latter case, they can become erect later (secondary perithallus) due to persistent growth. The species with lower *coxal* cells can also develop some filaments directed to the undersurface (subhypothallus) 2

1. Thallus erect (at least the gametophyte), without a dorsiventral symmetry. Plants not calcified. Structure different from above.. 28

2. Plants crustose, not calcified. Cells very small, usually ≤ 5 µm in diameter. Hypothallus with each cell dividing into an erect unbranched or sparsely branched filament. Secondary perithallus and subhypothallus absent. Rhizoids absent. Tetrasporangia developing from spherical or ovate conceptacles ....Family HILDENBRANDIACEAE
Genus *Hildenbrandia*........... 3

2. Plants crustose or not, calcified or not. Cells not very small, > 5 µm in diameter. Hypothallus with each cell dividing into one or more *coxal*, upper cells and, occasionally, one or more lower *coxal* cells. Perithallus erect or slightly inclined towards the margin. Secondary perithallus and subhypothallus sometimes present. Rhizoids present or absent. Tetrasporangia not developing from conceptacles, scattered or in sori 5

3. Genus *Hildenbrandia*
    3. Thallus rosy to dark red. Tetrasporangia ovoid, appearing cruciate or irregular, with non-parallel cleavage.. *H. rubra*
    3. Thallus brownish or purplish red. Tetrasporangia elongated, appearing zonate.............................. 4

4. Thallus brownish red. Conceptacle chamber spherical, with a small ostiole. Tetrasporangia with parallel, transverse or oblique cleavage, 5-10 × 20-30 µm.. *H. crouanii*

4. Thallus purplish red. Conceptacle chamber ovoid, with a large ostiole. Tetrasporangia always with transverse cleavage, 10-15 × 25-40 µm................. ....*H. occidentalis*

5. Hypothallus with some filaments larger than the others, appearing in surface view as a more or less conspicuous percurrent midrib and as a distinct central axis in cross section. Each hypothallial cell giving rise to more than one upper and one lower *coxal* cells. The filaments of the perithallus and subhypothallus are erect. Thallus not calcified. Gland cells are present, situated in the upper surface of the blade and apparent in surface view as white microscopic rounded spots.........Family RHIZOPHYLLIDACEAE
Genus *Contarinia* 6

5. Hypothallus either sparingly branched and more or less parallel (radially arranged), or much branched to form a polyflabellate layer (polyflabellately arranged), but not appearing as a distinct central axis in cross section. Each hypothallial cell giving rise to no more than one upper and one lower *coxal* cells. The filaments of the perithallus and subhypothallus are usually inclined towards the margin. Thallus calcified or not. Gland cells are absent 7

6. Genus *Contarinia*
    6. Plants are flattened, forming reniform and encrusting fronds, irregularly branched, with sinuous and lobed margins. In longitudinal section, hypothallial cells up to 35 (-40) µm long and 20 µm broad. Erect filaments up to 10-25 µm wide at basal parts. Gland cells ovoid or pyriform in cross section. Tetrasporangia cruciately arranged.......... ....*C. peyssonneliaeformis*
    6. Plants range from compressed to flattened, forming band-shaped segments almost regular in width (1-2 mm), irregularly dichotomously-distichously branched, with dentate margins. In longitudinal section, hypothallial cells up to 130 (-150) µm long and 60 µm broad. Erect filaments up to 30-45 µm at basal parts. Gland cells spherical. Tetrasporangia irregularly zonate.......*C. squamariae*

7. Each hypothallial cell cutting off a single upper *coxal* cell. Subhypothallus absent. Secondary perithallus absent. Plants fleshy, gelatinous. Carpogonial branch 2-3 celled. Tetrasporangia zonately arranged............ ....Family CRUORIACEAE
Genus *Cruoria*
C. cruoriaeformis

7. Each hypothallial cell cutting off either one single upper *coxal* cell, or one upper and one lower *coxal* cell, or one indiscriminately upper or lower *coxal* cell. Subhypothallus present or absent. Secondary perithallus present or absent. Plants gelatinous or firm and coriaceous. Carpogonial branch 3-6 celled. Tetrasporangia (when present) cruciately or irregularly cruciately arranged.. ....Family PEYSSONNELIACEAE.... 8

8. Thallus lacking rhizoids. Plants encrusting, entirely calcified. Each hypothallial cell cutting off one upper and one lower *coxal* cell. Secondary perithallus present.....................................Genus *Polystrata* 9

8. Thallus adhering to the substratum by rhizoids which arise along the whole of their undersurface. Plants foliose or encrusting, calcified or not. Each hypothallial cell dividing into either one upper and one lower *coxal* cell, or only one single upper *coxal* cell, or one indiscriminately upper or lower *coxal* cell. Secondary perithallus present or absent 10

9. Genus *Polystrata*

9. Subhypothallus not well developed, sometimes absent near the margins, up to 2 cells long (comprising the *coxal* cell). Perithallus cohesive after decalcification..................................*P. compacta*

9. Subhypothallus well developed, but a little shorter than perithallus. Perithallus loosely cohesive after decalcification...*P. fosliei*

10. In the centre of the thallus, the hypothallus gives rise only to a simple perithallus, but, near the margin, it gives rise also to a subhypothallus, due to the fact that the single *coxal* cell is situated indiscriminately at the upper or the lower part of the hypothallial cell. Thallus entirely calcified. Hypothallus polyflabellately arranged. Secondary perithallus present. Rhizoids one cell in length ....Genus *Metapeyssonnelia* *M. feldmannii*

10. The hypothallus generates only a single upper *coxal* cell. Subhypothallus usually absent, but, in some species, a lower *coxal* cell per hypothallial cell and a few developed subhypothallus can be also present. Thallus calcified or not. Hypothallus radially or polyflabellately arranged. Secondary perithallus present or absent. Rhizoids one or more cells in length. ....Genus *Peyssonnelia* 11

11. Genus *Peyssonnelia*

11. Thallus not calcified. Subhypothallus present. Hypothallus radially arranged. Rhizoids multicellular 12

11. Thallus calcified. Subhypothallus absent. Hypothallus radially or polyflabellately arranged. Rhizoids one or more cells long.......................... 13

12. Only one subhypothallial cell present (lower *coxal* cell). Rhizoids branched. Plants between 95 and 295 µm thick. Thallus membranous to cartilaginous in texture ....*P. squamaria*

12. Two subhypothallial cells present (including the lower *coxal* cell). Rhizoids unbranched. Plants between 155 and 385 µm thick. Thallus firm, cartilaginous to coriaceous in texture...*P. coriacea*

13. Thallus entirely calcified. Secondary perithallus present... 14

13. Thallus with hypobasal calcification and with or without cystoliths. Secondary perithallus present or absent 16

14. Rhizoids unicellular, unbranched. Plants with concentric growth zones from the marginal thallus meristem. Thallus ≤ 565 µm thick. Hypothallial cells ≤ 90 µm long.......*P. rosa-marina*...15

14. Rhizoids more than one cell long, usually branched. Plants without concentric growth zones from the marginal thallus meristem. Thallus ≤ 385 µm thick. Hypothallial cells ≤ 65 µm long ....*P. polymorpha*

15. Plants free-living, forming more or less globulous rhodoliths due to the occasional overturning of the plant on itself and the consequent change of its growing direction. The loose wrapping of the thallus delimits large cavities filled up with fine sediments ....*P. rosa-marina* f. *rosa-marina*

15. Plants growing on hard bottom, with a planar or slightly undulate frond...*P. rosa-marina* f. *saxicola*

16. Rhizoids one cell long. Cystoliths absent. Hypothallial cells radially or polyflabellately arranged... 17

16. Rhizoids more than one cell long. Cystoliths present or absent. Hypothallial cells radially arranged.. 27

17. Hypothallus polyflabellate.................................... 18

17. Hypothallus not distinctly polyflabellate 20

18. Perithallial filaments relatively free. Plants loose and gelatinous. Hypobasal calcification not well developed..*P. armorica*

18. Perithallial filaments laterally cohesive. Plants neither loose nor gelatinous. Hypobasal calcification well developed 19

19. Secondary perithallus present. Thallus 300-500 (– 800) µm thick. Tetrasporangia laterally inserted on the basal cell of the sterile filaments of the sori.... ....*P. codana*

19. Secondary perithallus absent. Thallus 70-125 µm thick. Tetrasporangia inserted at the apex of the *basal cell of the sterile filaments of the sori*.....*P. dubyi*

20. Angle of perithallus/hypothallus ≤ 50° 21

20. Angle of perithallus/hypothallus > 50° 23

21. Thallus ≤ 190 µm thick. Hypothallial cells ≤ 30 µm long. Secondary perithallus absent........*P. crispata*

21. Thallus up to 300 (-500) µm thick. Hypothallial cells usually > 30 µm long. Secondary perithallus present 22

22. Hypothallial cells 60-175 µm long. Rhizoids long ....*P. atropurpurea*

22. Hypothallial cells 25-80 µm long. Rhizoids short and globose..*P. magna*

23. Thallus ≤ 425 µm thick......................*P. harveyana*

23. Thallus ≤ 200 µm thick 24

24. Thallus ≥ 140 µm thick. Secondary perithallus present... 25

24. Thallus < 140 µm thick. Secondary perithallus absent or not well developed.................................. 26

25. Tetrasporangia inserted at the apex of the basal cell of the sterile filaments of the sori.......*P. rara-avis*

25. Tetrasporangia laterally inserted on the basal cell of the sterile filaments of the sori...............*P. hongii*

26. Hypobasal calcification well developed, to 70-110 µm thick. Secondary perithallus absent. Surface plane. Thallus firm, coriaceous, but fragile and broken easily..*P. stoechas*

26. Hypobasal calcification not well developed, to 45-70 µm thick. Secondary perithallus sometimes present but not well developed. Surface undulated. Thallus membranous to coriaceous, not fragile...... ....*P. inamoena*

27. Cystoliths present. Thallus ≤ 145 µm thick, membranous to cartilaginous in texture, whitish seen from below. Secondary perithallus absent. Hypobasal calcification up to 70 µm thick.....................*P. rubra*

27. Cystoliths absent. Thallus ≤ 300 µm thick, firm, coriaceous in texture, not whitish seen from below. Secondary perithallus present. Hypobasal calcification up to 240 µm thick..................................*P. bornetii*

28. Structure uniaxial. Growth by a single apical cell or by a small group of them 29

28. Structure multiaxial. Growth by a marginal meristem of many apical cells 50

29. Growth maintained by transverse division of a single apical cell. Thallus erect and bushy (at least the gametophyte). Tetrasporangia cruciately or zonately arranged 30

29. Growth by oblique division of a single apical cell or by a small group of them. Thallus erect, decumbent or prostrate. Tetrasporangia zonately arranged ... 41

30. Thallus is terete to flat. Plants rose pink in colour, mucilaginous and soft in texture. Structure consisting of a very apparent axial filament of elongated cells producing whorls of 3-4 repeatedly branched filaments composed of cells diminishing in size toward the periphery, where they are embedded in mucilage to form a loose cortex. In younger parts the whorls are distinct in surface view as annulations, but, in adult parts, the axial filament is usually surrounded by a compact layer of branched rhizoidal filaments produced by the periaxial cells and the bands are not distinct. Procarpic or non-procarpic. Carpogonial branch 3 or more cells long. Carposporophytes lacking involucre and ostiole. Spermatangia grouped on terminals or on subterminal cells of whorled branches. Tetrasporangia cruciately or zonately arranged 31

30. Thallus flattened. Plants dark red in colour, membranous to cartilaginous in texture. Structure different from above. Procarpic. Carpogonial branch 3-celled. Carposporophytes with a cellular pericarp, non ostiolate. Spermatangia in depressed sori. Tetrasporangia zonately arranged... 38

31. Plants are terete or flat.Whorls of 4 branched filaments. Procarpic. Auxiliary cell situated on a branch arising from the supporting cell. Outer cells moniliform............Family GLOIOSIPHONACEAE 32

31. Plants are terete or slightly compressed.Whorls of 3-4 branched filaments. Non-procarpic. Auxiliary cell not situated on a branch arising from the supporting cell. Outer cells moniliform or radially elongated...... 34

32. Plants flattened. Axes branching somewhat pinnate. Carpogonial branch 4-celled ....
....Genus *Schimmelmania*
S. ornata

32. Plants terete. Axes branching alternately or irregularly. Carpogonial branch 3-celled....................... 33

33. Outer cells not provided with terminal hair cells. Monocarpogonial. Auxiliary cell branch 2-celled, unbranched, with auxiliary cell intercalated...........
....Genus *Thuretella*
T. schousbœi

33. Outer cells occasionally provided with terminal hair cells. Mono- or polycarpogonial. Auxiliary branch usually 5-celled, occasionally branched from subtending cells, with auxiliary cell terminal..................
....Genus *Gloiosiphonia*
G. capillaris

34. Carpogonial branch 3-celled. Auxiliary cells numerous in cortex, indistinguishable before fertilization. Whorls of 3-4 branched filaments. Outer cells moniliform............Family CALOSIPHONACEAE 35

34. Carpogonial branches > 3 cells long. Auxiliary cells in special filaments, easily distinguishable before fertilization. Whorls of 4 branched filaments. Outer cells moniliform or radially elongated 37

35. Gonimoblast arising from the auxiliary cell. Outer cells always lacking terminal hyaline hairs...........
................................Genus *Calosiphonia*.......... 36

35. Gonimoblast arising from the connecting filament, near the auxiliary cell. Outer cells sometimes provided with hyaline hairs.................Genus *Schmitzia*
S. neapolitana

36. Genus *Calosiphonia*

36. Main axes usually simple, occasionally with some spine-like alternate or unilateral branches. Plants up to 2 (-4) cm high and 1-2 mm broad
....*C. dalmatica*

36. Main axes many times branched alternately. Plants up to 1-8 (-12) cm high and 2 mm broad ....
....*C. vermicularis*

37. Outer cortical cells moniliform, occasionally provided with terminal hyaline hairs. Carpogonial branches initially unbranched, latter producing opposite laterals to one or two orders, except for the carpogonium and its two subtending cells. Auxiliary cell branch 5-16 cells long, with auxiliary cell terminal...
.............................Family ACROSYMPHYTACEAE
Genus *Acrosymphyton*
A. purpuriferum

37. Outer cortical cells radially elongated, not provided with hyaline hairs. Carpogonial branches usually simple. Auxiliary cell branch 10-20-cells long, with auxiliary cell larger than the others, very distinct, intercalary, with the cells situated under and over it acting as nutritive cells
....................................Family DUMONTIACEAE
Genus *Dudresnaya*
D. verticillata

38. Plants dichotomously or laterally branched. Axial filament distinct throughout, surrounded by rhizoids, and the whole immersed in some layers of large rounded or elongated thick-walled and compacted cells. Cortex consisting of an outer part of several layers of moniliform cells arranged in radial rows, and a subcortex of slightly larger ovoid cells ...
...........................Family SPHAEROCOCCACEAE
Genus *Sphaerococcus*...... 39

38. Plants repeatedly pinnate branched, with alternating groups of 2-5 branchlets. Axial filament sometimes distinct throughout, immersed in some layers of large rounded or elongated thick-walled and compacted cells. Cortex of cells not arranged in radial rows..............................Family PLOCAMIACEAE
Genus *Plocamium*....... 40

39. Genus *Sphaerococcus*

39. Plants up to 4-5 cm broad, with a non conspicuous percurrent midrib. Larger medullary cells up to 60-70 µm in diameter. Outer cortical cells 10-15 µm in diameter in surface view............
....*S. rhizophylloides*

39. Plants up to 10-15 (-25) cm, lacking a midrib. Larger medullary cells up to 100-130 µm in diameter. Outer cortical cells 5-10 µm in diameter in surface view............................*S. coronopifolius*

40. Genus *Plocamium*

40. Main axis ⩽ 2000 μm broad. Ramuli and secondary branchlets and arrangement of ramuli along axes not always unilateral........*P. cartilagineum*

40. Main axis ⩽ 250 μm broad. Ramuli, secondary branchlets and arrangement of ramuli along axes unilateral......................................*P. secundatum*

41. Thallus flattened, usually complanately branched from the margins, lacking spine-like branchlets. Procarpic. Nutritive cells present...Family CYSTOCLONIACEAE.......... 42

41. Thallus terete or only slightly compressed, not complanately branched, sometimes bearing numerous spine-like branchlets. Procarpic or non-procarpic. Nutritive cells present or absent 45

42. Thallus erect, growing from a branched holdfast in the Mediterranean species. Plants cartilaginous in texture. Fronds not anastomosing. Growth by a single apical cell. Thallus transversed by a less-conspicuous axial filament, surrounded by several lacunose layers of longitudinally elongated cells.......................................Genus *Calliblepharis* 43

42. Thallus erect or somewhat prostrate, growing from a discoid holdfast. Plants thin and delicate, membranous when young and more firm in older specimens. Fronds occasionally anastomosed or fixed to other species by rhizoids produced secondarily from the frond surface. Growth by a small group of apical cells. Thallus appearing transverse by a diffuse axial filament in longitudinal section, and scarcely and irregularly celled in transverse section...Genus *Rhodophyllis* 44

43. Genus *Calliblepharis*

43. Thallus lanceolate, ≥ 10 mm wide. Blade is simple or irregularly branched. Marginal proliferations usually ⩽ 5 mm long, simple. Thallus ⩽ 650 μm thick. Axial filament surrounded by cells up to 50-200 μm longitudinally elongated up to 2 times their diameter. Cortex of 2-3 layers of pigmented cells.....................*C. ciliata*

43. Thallus linear-lanceolate, usually 2-6 mm broad. Blade dichotomous or irregularly branched. Marginal proliferations up to 15-30 mm long, sometimes hooked, especially those arising from the apex. Thallus up to 350 (-400) μm thick. Axial filament surrounded by cells from 50 μm to over 100 μm in diameter, longitudinally elongated up to 5 times their diameter. Cortex of a single layer of pigmented cells...*C. jubata*

44. Genus *Rhodophyllis*

44. Thallus up to 1-5 (-7) cm high and 1 cm wide, erect or somewhat prostrate..........*R. divaricata*

44. Thallus < 1 cm long and 2 mm wide, prostrate...*R. strafforellii*

45. Medullary cells with numerous secondary pit-connections. Procarpic. Auxiliary cell branch originating from the supporting cell and adjacent outwardly to the carpogonial branch, with intercalary auxiliary cell. Gonimoblast developing adjacent nutritive cells. Carposporophytes enclosed in a hemispherical poreless pericarp. Spermatangia formed in chains in outer cortical cells of short lateral branchlets. Tetrasporangia grouped in the swollen parts of special short lateral branchlets
....Family HYPNEACEAE
Genus *Hypnea*.........46

45. Medullary cells lacking secondary pit-connections. Non-procarpic. Auxiliary cell is a nearby cortical cell. Gonimoblast not developing adjacent nutritive-cells. Carposporophytes without pericarp, usually ostiolate. Spermatangia in clusters or rosettes on thallus surface. Tetrasporangia scattered or in sori on thallus surface...Family CAULACANTHACEAE........ 48

46. Genus *Hypnea*

46. Thallus ⩽ 3 cm high. Main axes ⩽ 800 μm in diameter.......................................*H. furnariana*

46. Thallus > 3 cm high. Main axes ≥1000 μm in diameter 47

47. Plants without definite main axes, 2-6 (-15) cm high and to (110-) 250-660 (-1000) μm in diameter. Main branches usually straight. In cross section, axial cells 20-40 (-65) μm in diameter, surrounded by cells ⩽ 160 μm wide. In longitudinal section, medullary cells ⩽ 250 μm long. ....*H. cervicornis*

47. Plants with main axis usually remaining conspicuous, 10-16 (-20) cm high and 1000 (-2000) μm in diameter. Main branches usually swollen and crozier-hooked. In cross section, axial cells 25-30 μm thick, surrounded by cells ⩽ 90 μm wide. In longitudinal section, medullary cells ⩽ 320 μm long............................*H. musciformis*

48. Branches segmented with elongated-ovoid internodes and constricted nodes. Segments terete to compressed. Cortex 2-5 cells thick. Growth by a single apical cell or by a small group of apical cells ....Genus *Catenella*
C. caespitosa

48. Branches not segmented, axes of constant diameter but pointed apices. Plant terete. Cortex one cell thick. Growth by a single apical cell................. 49

49. Medulla lacunose. Two periaxial cells per axial cell. Tetrasporangia scattered.........Genus *Caulacanthus*
C. ustulatus

49. Medulla not lacunose. Only one periaxial cell per axial cell. Tetrasporangia grouped in sori...Genus *Feldmannophycus*
F. rayssiae

50. Plants with a large, much-lobed supporting cell, that gives rise to several sterile (subsidiary) cells, similar in shape to the supporting cell. Carpogonial branch 2-celled, arising from the subsidiary cells. Plants flattened, foliose. Cortex of cells decreasing in size from the medulla outwards, not arranged in radial rows......Family KALLYMENIACEAE... 51

50. Plants without subsidiary cells. Carpogonial branch ≥ 2-celled, arising from the supporting cell. Plants flattened, compressed or terete. Cortex of cells sometimes arranged in radial rows........................ 58

51. Medulla compact, composed of large, rounded, thick-walled cells through which a delicate network of cobwebby filaments permeates, denser at the basal parts. Inner cortical cells ovoid to angular; outermost rounded. Procarpic. Supporting cell acting as auxiliary cell. Carposporophytes surrounded by sterile strands from the gametophytes, usually ostiolate ....Genus *Callophyllis*
C. laciniata

51. Medulla lax, filamentous, interwoven with very obvious stellate or ganglionic cells. Inner cortical cells stellate, the following large and angular or slightly stellate, and the outermost small, ovoid or irregularly shaped. Non-procarpic. Auxiliary cell systems with several subspherical to ovoid subsidiary cells on an ovoid auxiliary cell. Carposporophytes lacking filamentous involucre and ostiole 52

52. Gametophytes erect, with a simple or branched stipe from which arise a series of more or less alternately arranged blades. Plants strongly concave and auriculate at the base, the older blades enveloping the younger. Thallus dark red in colour; gelatinous and thin when young, and cartilaginous and thicker in older specimens. Medullar ganglionic cells present, yellow staining. Gametophytes and tetrasporophytes heteromorphic. Tetrasporangia zonately arranged ... .Genus *Meredithia*
M. microphylla

52. Thallus erect or somewhat decumbent, sessile or shortly stalked, broadly expanded above to form a single blade. Plants initially undivided, but adults can be lobed, laciniate or also irregularly dichotomously branched, sometimes perforated (not in Mediterranean species). Thallus rose-pink to dark red in colour, fleshy-membranous in texture. Medullar cells present, either ganglionic and yellow staining, or stellate and hyaline. Gametophytes and tetrasporophytes isomorphic. Tetrasporangia cruciately or irregularly arranged..........Genus *Kallymenia* 53

53. Genus *Kallymenia*

  53. Inner cortical cells ⩾ (40-)60 µm in diameter. Outer cortical cells rounded in surface view, and developing rosettes around large inner cells. Medullar cells stellate, usually colourless, $\gtrsim$ 50 µm large.. 54

  53. Inner cortical cells < 60 µm in diameter. Outer cortical cells ovoid, polyhedral or irregularly shaped in surface view, not forming rosettes around larger inner cells. Medullar cells ganglionic or stellate, yellow staining, usually < 50 µm large.. 55

  54. Thallus lobed. Inner cortical cells between 40-100 µm in greatest dimension. Medullar stellate cells with a rounded to ovoid body, (25-) 50-100 µm in diameter, and radiating arms ⩽ 300 µm long ....*K. feldmannii*

  54. Thallus laciniate and sometimes slightly pinnate at the ends. Inner cortical cells up to 70-185 µm in size. Medullar stellate cells with a very elongated body, to 70-230 µm long and 20-120 µm wide, and arms 20-115 µm in length originating mainly at distal parts of the cell......*K. lacerata*

  55. Frond irregularly, di- or trichotomously branched, reniform when very young. Outer cortical cells irregularly shaped...............................*K. patens*

  55. Frond simple, lobed or laciniate, sometimes with marginal proliferations. Outer cortical cells rounded, polyhedral or irregularly shaped 56

  56. Inner cortical cells up to 25-30 µm in diameter ....*K. spathulata*

  56. Inner cortical cells up to 40-50 µm in diameter 57

  57. Outer cortical cells rounded to ovoid or irregularly shaped in surface view. Medullary cells stellate or ganglionic in shape, with radiating arms ⩽ 320 µm in length. Polycarpogonial ....*K. reniformis*

  57. Outer cortical cells usually polyhedral in surface view, occasionally irregularly shaped. Medullar cells ganglionic, with radiating arms ⩽ 1000 µm in length. Monocarpogonial............*K. requienii*

58. Medulla compact, of hyaline cells....................... 59

58. Medulla lax, filamentous, occasionally with stellate or X-shaped cells (small ganglionic cells with body cell about twice the medullary filament diameter) remaining 65

59. Medulla of large cells with a core of small cells within. Plants membranous, terete, consisting of a prostrate and erect system of entangled and irregularly divided branches. Tetrasporangia in small ramuli, zonately arranged.........Genus *Wurdermannia*
W. miniata

59. Medulla lacking a core of small cells. Plants cartilaginous, compressed or flattened, erect, usually dichotomously or irregularly dichotomously branched. Tetrasporangia not in small ramuli, cruciately arranged...........Family PHYLLOPHORACEAE 60

60. Cortex of several layers of small isodiametric cells mostly arranged in radial rows. Plants compressed, shortly stipitate, dividing in one plane. Life history biphasic, with tetrasporophytes hemiparasitic, as pustules on the surface of female gametophytes ....Genus *Gymnogongrus* 61

60. Cortex of small cells not arranged in radial rows. Plants flattened, with a long stipe, not complanately branched. Life cycle triphasic with isomorphic gametophytes and tetrasporophytes 62

61. Genus *Gymnogongrus*

  61. Thallus up to 5-7 (-15) cm high, and 2-4 mm broad. Apices obtuse. Medullar cells 100-250 µm and 2-3 times longer. Pustule small in proportion to branches, scattered over both surfaces...*G. crenulatus*

  61. Thallus up to 2.5 (-5) cm high and 0.5-0.6 mm broad, except in bifurcations, which are 0.8-1.1 mm wide. Apices acute. Medullar cells 10-20 µm, and 4-8 (10) times longer. Pustule large in proportion to branches, sometimes completely encircling them..........................*G. griffithsiae*

62. Thallus arising from a branched cylindrical rhizomatous holdfast. Midrib absent. Carpogonial branches situated in the blade surface. Tetrasporangia aggregated in a series of sequentially developing sori that protrude as bands on both surfaces of frond........ ....Genus *Schottera*
S. nicaeensis

62. Plants arising from a discoid holdfast. Midrib-like thickening present in some species. Carpogonial branches situated in special bladelets. Tetrasporangia in elevated sori, not sequentially developed ....Genus *Phyllophora*.... 63

63. Genus *Phyllophora*

  63. Stipe short in relation to total length of the plant. Blade more or less parallel-sided. Margin undulated. Thallus with a basal or medium midrib-like thickening formed by secondary growth of the cortical layer..............*P. crispa*

63. Stipe long in relation to total length of the plant. Blade more or less fan-shaped. Margin plane. Thallus lacking midrib-like thickening.........64

64. Blade very divided, with acute apices. Stipe usually representing up to half of the total length of the frond. Medullary cells up to 40-50 µm in diameter.................................*P. heredia*

64. Blade usually with a single dichotomy and obtuse apices. Stipe usually less than one third of total length of the frond. Medullary cells ≤ 90 µm in diameter....................................*P. sicula*

65. Outer cortex arranged in filamentous fascicles. Non-procarpic... 66

65. Outer cortex not arranged in filamentous fascicles. Procarpic or non-procarpic.................................... 70

66. Carpogonial branch with adjacent nutritive auxiliary cells (nutritive cells originating from the same branch system of the carpogonial branch)............... ....Family SCHIZYMENIACEAE.. 67

66. Carpogonial branch without adjacent nutritive auxiliary cells.......Family NEMASTOMATACEAE . 68

67. Gland cells rounded to ovoid in shape formed in an intercalary position in cortical fascicles. Gametophytes erect or somewhat decumbent, the branching is dichotomous or irregularly lobed or palmate to pinnate. Branches often anastomosing. Carposporophytes lacking a filamentous involucre................... ....Genus *Platoma*
P. cyclocolpum

67. Gland cells ellipsoid to ovoid in shape, situated at the end of the cortical filaments. Gametophytes erect, simple or irregularly lobed, sometimes laciniate. Branches not anastomosing. Carposporophytes with a filamentous involucre......................... ....Genus *Schizymenia*
S. dubyi

68. Gland cells present in gametophytes of Mediterranean species. Fronds gelatinous but cartilaginous at the base. Auxiliary cell without nutritive cells. Gonimoblasts developing from the connecting filament. ....Genus *Nemastoma*
N. dichotomum

68. Gland cells absent in gametophytes of Mediterranean species. Fronds soft and mucilaginous, very delicate. Auxiliary cell bearing short simple or branched chains of subspherical nutritive cells. Gonimoblast developing either on auxiliary cells or on connecting filaments near the point of union with auxiliary cell ....Genus *Predaea*..... 69

69. Genus *Predaea*

69. Plants up to 4-5 (-9) cm high, dichotomously or irregularly branched. Outer cortical cells ovoid to cylindrical. Carpogonial branch 2-celled. Nutritive cells originating in groups of (3-) 5-12 (-15) cells, situated on the cells site under and over the auxiliary cell. Gonimoblast developing on a lateral swelling of the junction filament, the gonimoblast and the connecting filament remaining side by side. Gonimoblast rounded or sometimes pyriform, radially orientated............ ....*P. ollivieri*

69. Plants up to 1-4 (-7) cm high, simple or sparsely branched dichotomously or irregularly at the apices. Outer central cells cylindrical. Carpogonial branch 3-celled. Nutritive cells originating in groups of 1-5 per bearing cell, in close related cells, but not always in the upper and the lower part of the auxiliary cell. Gonimoblast initially formed on the auxiliary cell, and originating opposite to the connecting filament. Gonimoblast ovoid to lobed......................................*P. pusilla*

70. Carpogonial and auxiliary branches in a special compact branch system (ampulla). Non-procarpic. Tetrasporangia cruciately arranged ....Family HALYMENIACEAE....71

70. Carpogonial and auxiliary branches not in a special compact branch system (ampulla). Procarpic or non-procarpic. Tetrasporangia cruciately or zonately arranged.. 80

71. Cortex of cells arranged in radial rows. Inner cortical cells ovoid to ameboid. Medulla filamentous, with numerous X-shaped cells remaining......... 72

71. Cortex not in radial rows. Inner cortical cells stellate and lying in the plane of the flattened surface. Medulla filamentous but lacking X-shaped cells... 76

72. Margin rolled over one of the sides giving a concave-convex appearance. Plants segmented, rigid, sometimes spirally twisted..Genus *Acrodiscus*
A. vidovichii

72. Margin not rolled over one of the sides. Plants not segmented, not rigid, not spirally twisted...........73

73. Thallus with a canaliculated margin in the Mediterranean species, sometimes distinct only with a magnifying glass. Plants simple, flattened ....Genus *Aeodes*
A. marginata

73. Margin not canaliculated. Plants simple or variously divided, flattened or compressed............................. ....Genus *Grateloupia*.... 74

74. Genus *Grateloupia*

74. Thallus flattened, foliose, simple or deeply divided once to several times, often proliferous from damaged or truncated parts. Plants 2-6 cm wide...*G. doryphora*

74. Thallus compressed, not foliose, dichotomously or pinnately branched. Plants ≤ 5 mm broad 75

75. Frond branching repeatedly dichotomous. Plants up to 1.5-3.0 mm wide, attenuated towards the outer surface..............*G. dichotoma*

75. Frond initially dichotomous and becoming largely complanately branched, bi- or tripinnate when old. Plants up to 3 (-5) mm wide........... ....*G. filicina*

76. Medulla lax in young parts, with filaments forming bridges from cortex to cortex. Thallus simple or variously branched. Stipe filamentous. Thallus usually rose pink in colour, very soft and gelatinous in texture. Carposporophyte and tetrasporangia scattered and immersed in outer cortex................................ .... Genus *Halymenia*...77

76. Medulla usually fairly compact and strong, without filaments forming bridges from cortex to cortex. Thallus leaf-like, with proliferations of the same shape of the main blade, with the thallus appearing catenate. In cross section, the stipe is celled, with a secondary developed cortex arranged in concentric circles. Thallus dark-red in colour, membranous to cartilaginous in texture.

Carposporophyte and tetrasporangia scattered or occurring in secondary bladelets ....Genus *Cryptonemia*.... 79

77. Genus *Halymenia*

77. Plants terete or slightly compressed, dichotomously or subdichotomously branched, sometimes whorled. Medulla lax, with occasionally transversely orientated filaments. When the thallus is folded, creases are formed.......*H. trigona*

77. Thallus flattened, simple, pinnate or dichotomously branched. Medulla lax in young parts with many to most filaments transversely orientated, dense and irregular in older parts. When the thallus is folded, creases are not formed. 78

78. Thallus lanceolate, simple or, rarely, divided once dichotomously. Plants up to 180 (-300) µm thick. Medullar filaments unbranched, 8-14 µm thick. Outer cortical cells polyhedral in surface view, compact, ≤ 15 µm in greatest dimension ....*H. latifolia*

78. Thallus complanately much-branched to 4-5 orders, pinnate or occasionally subdichotomous. Plants ≤ 800 µm thick. Medullar filaments branched, of 2 sizes, 10-15 and 15-20 µm. Outer cortical cells ovoid in surface view, ≤ 10 µm in diameter, and radially elongated (up to 10-15 µm high) ....*H. floresia*

79. Genus *Cryptonemia*

79. Blades ≤ 3 cm broad, into which the stipe extends as an evanescent midrib-like thickening in mature plants ....*C. lomation*

79. Blades ≤ 0.5 cm broad. Midrib absent.............. ....*C. tunaeformis*

80. Cortex of cells arranged in radial rows. Inner cortical cells ovoid to ameboid. Medulla of a network of irregularly oriented filaments and numerous X-shaped cells remaining. Thallus erect or decumbent. Procarpic or non-procarpic....................................81

80. Cortex of cells not arranged in radial rows. Inner cortical cells stellate and lying in the plane of the flattened surface. Medulla filamentous, lacking X-shaped cells, but occasionally with some stellate cells remaining. Thallus erect. Non-procarpic....84

81. Medulla consisting of primary filaments, usually longitudinally orientated, interlined with some secondary short filaments, 1-3 cells long, thinner, usually transversely oriented. Procarpic.................. ....Family GIGARTINACEAE
Genus *Chondracanthus*.....82

81. Medulla lacking secondary filaments. Procarpic or non-procarpic...83

82. Genus *Chondracanthus*

82. Fronds compressed or terete, irregularly branched. Plants erect or decumbent, often arching and reattaching on contact...........*C. acicularis*

82. Fronds flattened, regularly pinnately branched. Plants erect, not reattaching ....*C. teedii*

83. Margin ribbed and dentate. Thallus leafy and simple or dichotomously branched. Procarpic. Plants midlittoral ....Family RISSOELLACEAE
Genus *Rissoëlla*
R. verruculosa

83. Margins smooth or ribbed, but not dentate. Thallus almost as long as it is broad, lobed. Non-procarpic. Plants sublittoral ....Genus *Chondrymenia*
C. lobata

84. Medulla lax, in younger parts transversed by a network of filaments mostly at right angles to plane of the flattened surface, and dense and transversely oriented in older ones. Cortex thin. Outer cortical cells radially elongated. Gland cells absent ....Family FURCELLARIACEAE...85

84. Medulla appearing empty in younger part, and transversed by a network of filaments mostly at right angles to plane of the flattened surface in older ones, usually with numerous stellate cells remaining. Cortex thick. Outer cortical cells not radially arranged. Gland cells sometimes present ....Family SEBDENIACEAE
Genus *Sebdenia*...86

85. Fronds bearing a long, terete and caulescent stipe, usually branched in mature plants, with an inner part filamentous, and an outer part of little and radially elongated cells. Plants flattened, with blades broader than high and peltate. Plants cartilaginous....... ....Genus *Neurocaulon*
N. foliosum

85. Fronds lacking a caulescent branched stipe. Plants compressed or flattened (subcylindrical when narrow), entire or irregularly dichotomously branched, often furnished with ligulate proliferations from the margins and blade surface. Thin plants soft and diaphanous, gelatinous; thicker plants subcartilaginous ....Genus *Halarachnion*
H. ligulatum

86. Genus *Sebdenia*

86. Refringent gland cells present. Medullary stellate cells abondant..87

86. Gland cells absent. Medullary stellate cells rare. ....*S. monardiana*

87. Gland cells very obvious situated in the center of the stellate cells and 20-30 µm in diameter, or over the medullar filaments, and then 15-20 µm thick. Thallus 400-500 µm thick, cuneiform, thicker at the base and margins, first simple and lanceolate, later divided in large subdichotomous lobes, with deep sinus. Margin whole. Stellate cortical cells 20-50 (-70) µm in diameter..*S. rodrigueziana*

87. Gland cells not obvious, situated in the center of the stellate cells and 10-15 µm in diameter. Thallus ≤ 1500 µm thick, more or less flattened, but usually cylindrical at the apices, dichotomously or subdichotomously branched, usually with marginal proliferations. Stellate cortical cells up to 15-20 (-25) µm in diameter... ....*S. dichotoma*

TAXONOMIC ARRANGEMENT OF THE GENERA TREATED

Order GIGARTINALES Schmitz *in* Engler

Family ACROSYMPHYTACEAE Lindstrom
Genus *ACROSYMPHYTON* Sjöstedt; *"Acrosymphytonema" stadium* Boudouresque, Perret-Boudouresque & Knoepffler-Péguy
A. purpuriferum (J. Agardh) Sjöstedt
Tetrasporophyte: *"Acrosymphytonema breemaniae"* Boudouresque, Perret-Boudouresque & Knoepffler-Péguy

Family CALOSIPHONIACEAE Kylin
Genus *CALOSIPHONIA* P.L. Crouan & H.M. Crouan
C. dalmatica (Kützing) G.B. De Toni
C. vermicularis (J. Agardh) Schmitz
Genus *SCHMITZIA* Lagerheim ex P.C. Silva
S. neapolitana (Berthold) Lagerheim ex P.C. Silva
Family CAULACANTHACEAE Kützing
Genus *CATENELLA* Greville
C. caespitosa (Withering) Irvine *in* Parke & P.S. Dixon
Genus *CAULACANTHUS* Kützing
C. ustulatus (Turner) Kützing
Genus *FELDMANNOPHYCUS* Augier & Boudouresque
F. rayssiae (J. Feldmann & G. Feldmann) Augier & Boudouresque
Family CRUORIACEAE Kylin
Genus *CRUORIA* Fries
C. cruoriaeformis (P.L. Crouan & H.M. Crouan) Denizot
Family CYSTOCLONIACEAE Kützing
Genus *CALLIBLEPHARIS* Kützing
C. ciliata (Hudson) Kützing
C. jubata (Goodenough & Woodward) Kützing
Genus *RHODOPHYLLIS* Kützing
R. divaricata (Stackhouse) Papenfuss
R. strafforellii Ardissone
Family DUMONTIACEAE Bory de Saint-Vincent
Genus *DUDRESNAYA* P.L. Crouan & H.M. Crouan
D. verticillata (Withering) Le Jolis
Family FURCELLARIACEAE Greville
Genus *HALARACHNION* Kützing
H. ligulatum (Woodward) Kützing
Tetrasporophyte: *Cruoria rosea* P.L. Crouan & H.M. Crouan
Genus *NEUROCAULON* Zanardini ex Kützing
N. foliosum (Meneghini) Zanardini
Family GIGARTINACEAE Kützing
Genus *CHONDRACANTHUS* Kützing
C. acicularis (Roth) Fredericq *in* Hommersand, Guiry, Fredericq & Leister
C. teedii (Mertens ex Roth) Kützing
Family GLOIOSIPHONACEAE Schmitz
Genus *GLOIOSIPHONIA* Carmichael *in* Berkeley
G. capillaris (Hudson) Carmichael *in* Berkeley
Tetrasporophyte: *Rhodadiscus pulcherrimus* P.L. Crouan & H.M. Crouan
Genus *THURETELLA* Schmitz
T. schousbœi (Thuret) Schmitz
Genus *SCHIMMELMANNIA* Schousboe ex Kützing
S. ornata Schousboe ex Kützing
Family HYPNEACEAE J. Agardh
Genus *HYPNEA* Lamouroux
H. cervicornis J. Agardh
H. furnariana Cormaci, Alongi & Dinaro
H. musciformis (Wulfen) Lamouroux
Family KALLYMENIACEAE (J. Agardh) Kylin
Genus *CALLOPHYLLIS* Kützing
C. laciniata (Hudson) Kützing
Genus *KALLYMENIA* J. Agardh
K. feldmannii Codomier
K. lacerata J. Feldmann
K. patens (J. Agardh) Parkinson
K. reniformis (Turner) J. Agardh
K. requienii J. Agardh
K. spathulata (J. Agardh) Parkinson
Genus *MEREDITHIA* J. Agardh
M. microphylla (J. Agardh) J. Agardh
Tetrasporophyte: *Rhodochorton hauckii* (Schiffner) Hamel
Family NEMASTOMATACEAE Schmitz *in* Engler
Genus *NEMASTOMA* J. Agardh
N. dichotomum J. Agardh
Genus *PREDAEA* G. De Toni
P. ollivieri J. Feldmann
P. pusilla (Berthold) J. Feldmann
Family PEYSSONNELIACEAE Denizot
Genus *METAPEYSSONNELIA* Boudouresque, Coppejans & Marcot
M. feldmannii Boudouresque, Coppejans & Marcot
Genus *PEYSSONNELIA* Decaisne
P. armorica (P.L. Crouan & H.M. Crouan) Börgesen
P. atropurpurea P.L. Crouan & H.M. Crouan
P. bornetii Boudouresque & Denizot
P. codana (Rosenvinge) Denizot
P. coriacea J. Feldmann
P. crispata Boudouresque & Denizot
P. dubyi P.L. Crouan & H.M. Crouan
P. harveyana P.L. Crouan & H.M. Crouan
P. hongii Marcot-Coqueugniot
P. inamoena Pilger
P. magna Ercegovic
P. polymorpha (Zanardini) Schmitz *in* Falkenberg
P. rara-avis Marcot & Boudouresque
P. rosa-marina Boudouresque & Denizot
f. *rosa-marina* Boudouresque & Denizot
f. *saxicola* Boudouresque & Denizot
P. rubra (Greville) J. Agardh
P. squamaria (Gmelin) Decaisne
P. stoechas Boudouresque & Denizot
Genus *POLYSTRATA* Heydrich
P. compacta (Foslie) Denizot
P. fosliei (Weber-van-Bosse) Denizot
Family PHYLLOPHORACEAE Nägeli
Genus *GYMNOGONGRUS* Martius
G. crenulatus (Turner) J. Agardh
G. griffithsiae (Turner) Martius
Genus *PHYLLOPHORA* Greville
P. crispa (Hudson) Dixon
P. heredia (Clemente y Rubio) J. Agardh
P. sicula (Kützing) Guiry & Irvine
Genus *SCHOTTERA* Guiry & Hollenberg
S. nicaëensis (Lamouroux *ex* Duby) Guiry & Hollenberg
Family RHYZOPHYLLIDACEAE Schmitz
Genus *CONTARINIA* Zanardini
C. peyssonneliaeformis Zanardini
C. squamariae (Meneghini) Denizot
Family RISSOËLLACEAE Kylin
Genus *RISSOËLLA* J. Agardh
R. verruculosa (Bertoloni) J. Agardh
Family SARCODIACEAE Kylin
Genus *CHONDRYMENIA* Zanardini
C. lobata (Meneghini) Zanardini
Family SCHIZYMENIACEAE (Schmitz & Hauptfleisch) Masuda & Guiry
Genus *PLATOMA* Schousboe ex Schmitz
P. cyclocolpum (Montagne) Schmitz
Genus *SCHIZYMENIA* (J. Agardh) J. Agardh
S. dubyi (Chauvin ex Duby) J. Agardh

Tetrasporophyte: *Haematocelis rubens* J. Agardh

Family SPHAEROCOCCACEAE Dumortier emend. Searles

Genus *SPHAEROCOCCUS* Stackhouse

S. coronopifolius (Goodenough & Woodward) Stackhouse

Tetrasporophyte: *Haematocelis fissurata* P.L. Crouan & H.M. Crouan

S. rhizophylloides Rodríguez Femenías

Order HALYMENIALES Saunders & Kraft

Family HALYMENIACEAE Bory de Saint-Vincent

Genus *ACRODISCUS* Zanardini

A. vidovichii (Meneghini) Zanardini

Genus *AEODES* J. Agardh

A. marginata (Roussel ex Montagne) Schmitz

Genus *CRYPTONEMIA* J. Agardh

C. lomation (Bertoloni) J. Agardh

C. tunaeformis (Bertoloni) Zanardini

Genus *GRATELOUPIA* C. Agardh

G. dichotoma J. Agardh

G. doryphora (Montagne) Howe

G. filicina (Lamouroux) C. Agardh

Genus *HALYMENIA* C. Agardh

H. floresia (Clemente y Rubio) C. Agardh

H. latifolia P.L. Crouan & H.M. Crouan

H. trigona (Clemente y Rubio) C. Agardh

Family SEBDENIACEAE Kylin

Genus *SEBDENIA* (J. Agardh) Berthold

S. dichotoma (J. Agardh) Berthold

S. monardiana (Montagne) Berthold

S. rodrigueziana (J. Feldmann) Codomier

Order HILDENBRANDIALES Pueschel & Cole

Family HILDENBRANDIACEAE Rabenhorst

Genus *HILDENBRANDIA* Nardo

H. crouanii J. Agardh

H. occidentalis Setchell *in* Gardner

H. rubra (Sommerfelt) Meneghini

Order PLOCAMIALES Saunders & Kraft

Family PLOCAMIACEAE Kützing

Genus *PLOCAMIUM* Lamouroux

P. cartilagineum (Linnaeus) P.S. Dixon

P. secundatum (Kützing) Kützing

INCERTAE SEDIS

Genus *WURDERMANNIA* Harvey

W. miniata (Sprengel) J. Feldmann & Hamel

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ANALYSE D'OUVRAGE/*BOOK REVIEW*

M. NORMAN, 2000. Cephalopods – a world guide. ConchBooks (E-mail : conchbooks@conchbooks.de), D-55546 Hackenheim (Allemagne). p., 708 fig., 16 × 24 cm. Couverture : carton rigide plastifié. 41.00 Euros (+ frais d'expédition en Europe : 5.50 Euros). [Demander les conditions de vente pour l'édition en Allemand].

Depuis la parution, en 1987, du grand livre des Céphalopodes rédigé et illustré par Kir. N. Nesis (« Cephalopods of the World »), les teuthologistes et les naturalistes amateurs s'intéressant aux Poulpes, Seiches, Sépioles et Calmars, attendaient un ouvrage faisant « systématiquement » appel aux photos en couleur. L'excellent livre de Norman répond pleinement à cette attente, en présentant près de 230 espèces par une véritable galerie de portraits d'animaux vivants – pour la plupart photographiés dans leur environnement naturel. Dans un avant-propos enthousiaste, Kir Nesis insiste sur l'importance de cette approche : « [les céphalopodes] sont difficiles à identifier quand ils sont morts, voire fixés, alors qu'ils sont très différents entre eux dans leur environnement naturel, grâce aux couleurs et comportements si diversifiés ».

Afin de permettre au lecteur non initié de se familiariser avec ces animaux, Norman commence par une introduction se terminant par un glossaire, continue par une brève description des caractéristiques de la classe des Céphalopodes, avec un survol de la systématique – d'ailleurs bien visualisée dès le sommaire – couvrant les différents groupes, en ajoutant un bref rappel sur les formes fossiles. Pour chaque groupe taxonomique, une brève introduction présente l'essentiel de sa répartition géographique et de sa biologie/écologie, avec des renvois à une ou plusieurs des 35 « histoires illustrées [picture stories] ». Ces histoires offrent des observations inédites ou peu connues, qui sont autant de suggestions pour des études futures.

Contrairement aux compilations plus ou moins réussies de certains « éditeurs d'images », Norman offre un véritable précis de teuthologie, richement illustré, avec un index des noms scientifiques et vernaculaires ; en même temps il attire l'attention du lecteur (et en particulier du plongeur scientifique) sur les nombreuses questions non encore résolues. Ainsi 20 espèces de Poulpes non encore décrites « lege artis » (ce qui exigerait le dépôt d'un ou de plusieurs spécimens types) sont représentées par d'excellentes photos accompagnées de brèves descriptions biologiques –voilà un exemple de ce que Nesis dit dans son avant-propos !

Ce très beau livre témoigne d'un souci permanent de soigner le contenu autant que l'esthétique. L'auteur, un scientifique de renom international, a su créer, avec le concours d'une maison d'édition spécialisée dans le domaine du livre naturaliste, un guide « haut de gamme ».

M. NORMAN & A. REID, 2000. A Guide to Squid, Cuttlefish and Octopuses of Australasia. CSIRO Publishing (E-mail : sales@publish.csiro.au), 150 Oxford Street, Collingwood, Victoria 3066 (Australie). 96 p., 242 figs, 16.5 x 24 cm. Couverture : carton souple plastifié. 32.00 $AU.

Bien que ce guide soit le « petit frère » de CEPHALOPODS ñ A WORLD GUIDE, il peut être utilisé de manière parfaitement indépendante, pour identifier la soixantaine d'espèces de Céphalopodes recensés sur les côtes Australiennes et dans les régions avoisinantes comprises entre 10ºN et 50ºS, et entre 95º et 190ºE.

L'introduction est suivie de brefs rappels sur (1) le rapport systématique entre les Céphalopodes et les autres Mollusques, (2) l'évolution des Céphalopodes, (3) leur importance dans la faune marine actuelle, (4) les grands groupes de Céphalopodes vivants et l'essentiel de leur biologie.

A quelques exceptions près, la présentation de chaque espèce occupe une page entière : une grande photo en couleur montrant l'adulte, une ou deux petites photos consacrées à un détail morphologique ou de comportement, toutes avec de brèves légendes, un texte succinct indiquant le mode de vie, la taille adulte, quelques caractéristiques de la reproduction, puis un cartouche contenant les caractères distinctifs de l'espèce et une petite carte montrant sa répartition géographique.

Pour une trentaine d'espèces de Seiches, l'os (sépion) est présenté en vues dorsale et ventrale ; ces « portraits de pièces détachées » sont réunis dans une série de planches qui seront particulièrement appréciées par les collectionneurs fréquentant les plages. En effet, les sépions, détachés du corps après la mort de l'animal, peuvent s'échouer sur une plage, à l'issue d'une dérive plus ou moins longue ; ils sont alors des indicateurs intéressants, quoique « approximatifs », de la présence d'une ou de plusieurs espèces de seiches dans une zone plus ou moins vaste.

Notons enfin l'excellent glossaire ainsi que l'index réunissant les noms scientifiques et vernaculaires. Tout comme son « grand frère » le « Guide mondial des Céphalopodes », ce fascicule est un excellent outil de travail doté d'une grande qualité esthétique.

S. v. Boletzky

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COMMUNITY STRUCTURE OF PARASITIC HELMINTHS OF BIRDS OF THE GENUS *LARUS* FROM MAR DEL PLATA, ARGENTINA

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PARASITES
HELMINTHS
COMMUNITY STRUCTURES
LARUS SPP.

ABSTRACT. – Community structure of parasite helminths of *L. dominicanus* (Lichtenstein, 1823), *L. maculipennis* (Lichtenstein, 1823) and *L. cirrocephalus* (Vieillot, 1818) were studied. Species richness of the three helminthological communities was composed by 11 species (4 digenean, 5 cestodes and 2 nematodes). The nematode *Pectinospirura argentata* (Wehr, 1933) was the central species of the helminthological community of *L. dominicanus* and the digenean *Tanaisia (Tanaisia) fedtschenkoi* Skrjabin, 1924 of *L. maculipennis* and *L. cirrocephalus* respectively. The similitude between helminthological communities of *L. dominicanus-L. maculipennis* was 62.54 %; between *L. dominicanus-L. cirrocephalus* it was 61.54 %, and between *L. maculipennis-L. cirrocephalus*: 61.54 %. In *L. dominicanus* all associations between intestinal species were significative with the exception of *Alcataenia dominicana* Spasskaja, 1971– *Paricterotaenia porosa* (Rudolphi, 1810); *Stephanoprora denticulata* (Rudolphi, 1802) Odhner, 1911-*Tetrabothrius argentinus* (Szidat, 1964) and *T. argentinus-Paricterotaenia porosa* were significative in *L. maculipennis* and *L. cirrocephalus* respectively. Two site shifting cases were observed between *Tetrabothrius argentinus-Paricterotaenia porosa* and *T. argentinus-Alcataenia dominicana.*

PARASITES
HELMINTHES
STRUCTURE DES COMMUNAUTÉS
LARUS SPP.

RÉSUMÉ. – Les communautés d´Helminthes de *Larus dominicanus* (Lichtenstein, 1823), *L. maculipennis* (Lichtenstein, 1823) et *L. cirrocephalus* (Vieillot, 1818) ont été étudiées. La richesse spécifique est de 11 espèces (4 Digènes, 5 Cestodes et 2 Nématodes). Le Nématode *Pectinospirura argentata* Wehr, 1933 est l'espèce centrale dans la communauté helminthologique de *L. dominicanus* et le Digène *Tanaisia (Tanaisia) fedtschenkoi* Skrjabin, 1924 celle des communautés helminthologiques de *L. cirrocephalus* et *L. maculipennis*. Les similitudes entre les communautés helminthologiques de *L. dominicanus-L. maculipennis, L. dominicanus-L. cirrocephalus* et *L. maculipennis-L. cirrocephalus* sont de 62.54 %, 61.54 % et 61.54 % respectivement. Les associations d'espèces intestinales chez *L. dominicanus* sont significatives sauf celle d'*Alcataenia dominicana* Kolotilova, 1971-*Paricterotaenia porosa* (Rudolphi, 1810). Les associations *Stephanoprora denticulata* (Rudolphi, 1802) Odhner, 1911-*Tetrabothrius argentinus* (Szidat, 1964) et *T. argentinus-P. porosa* sont significatives chez *L. maculipennis* et *L. cirrocephalus* respectivement. Deux changements de site ont été observés entre *T. argentinus-P. porosa* et *T. argentinus-A. dominicana.*

INTRODUCTION

Birds of the family Laridae are one of the components in the coastal fauna of the argentine Sea. They have been frequently studied, in particular those belonging to the genus *Larus* Linné (Magno 1971, Canevari *et al.* 1991, Lizurume *et al.* 1995). The genus in question is represented in Argentina by six species (Canevari *et al.* 1991) among which are *Larus dominicanus* (Lichstenstein, 1823); *L. maculipennis* (Lichstenstein, 1823) and *L. cirrocephalus* (Vieillot, 1818). Although these three seagull species are inshore coastal species, they go upriver and may be found in pools and wetlands. These birds have a highly varied diet, eating insects, small invertebrates and fishes which may come from inland water bodies, marine coasts, rural areas, debris collected near the sea, and eggs of other species of marine birds. Therefore, they are considered as secondary and tertiary predators in the food web. The previous statement suggests that the study of bird parasites contributes to assess the state of the marine ecosystem, among others. Still, although in the North Hemisphere there are papers about helminth parasites of several *Larus* species focused on systematics and ecology (Bakke 1972, 1985, Hoberg 1996, Galaktionov 1996) in the South Hemisphere only fauna inventories carried out by Torres *et al* (1982, 1983, 1991, 1992) for Chile and only systematic information (Szidat 1964, Cremonte & Navone 1998) for Argentina are known. Therefore, the goals of this work are: 1) determining the parasitic community structure of *Larus dominicanus*, *L. maculipennis* and *L. cirrocephalus* at the inshore coastal region of Mar del Plata; 2) calculating by means of the species richness of the three helminth communities the degree of likeness between them; 3) establishing the existence of areal associations between gut species and those appearing frequently together; and 4) study gut helminth distribution with the aim of estimating species *site* occupation percents and detecting possible cases of shifting.

MATERIAL AND METHODS

Between 1995-1998, 44 specimens of seagulls of the genus *Larus* were caught in the outskirts of Mar del Plata city (38º05'S – 57º38'W), General Pueyrredón District, Buenos Aires Province. Nine of these birds belong to the *L. dominicanus* species, 26 to *L. maculipennis* and 9 to *L. cirrocephalus*. After describing the composition of the helminthological fauna by means of the study of systematics (Labriola & Suriano, in press) of collected parasites, total percent of general parasitosis, total percent of seagulls infected with one or more helminth species and parasitosis percent for each helminth group (considering digeneans, cestodes and nematodes as groups) were calculated. For each helminth species found in each host species, prevalence, mean intensity, parasite frequency or dominance, and abundance were estimated, according to Margolis *et al.* 1982 and Bush *et al.* 1997. Helminth community structures for each studied seagull species were established according to Esch *et al.* 1990. Species frequencies higher than 45 % were considered as central species; species with frequencies between 10 %-45 % were considered as secondary species and species with frequencies lower than 10 % were considered as satellite species. Sorensen similitude coefficient (Morales y Pino 1987) were estimated as a function of species richness of each of the three helminth communities with the aim of expressing the degree of likeness between community pairs in a percentual scale. The Fager Affinity Index (Morales y Pino 1987) and a t-test to evaluate its significance level were used to establish the existence of a real association between gut species frequently associated, independently of its abundances. This index was chosen according to the criterion stated by Combes (1983) in the sense that in low prevalence cases, as presently occurs and as frequently found on analyzing helminths parasitic on wildlife, it is convenient to use association indices not including double absences, because they are very common. *Site* occupation percents were estimated to assess helminth species distribution along the guts of seagulls and to detect possible shiftings. For this purpose, the gut was divided in five sections: Duodenum I, Duodenum II, Ileum I, Ileum II and Rectum. For cestodes, the chosen site was defined as the area of scolex attachment according to Bakke (1985).

RESULTS

Percent of parasitism of host seagulls was high. Of all birds examined (44) 84.90 % had parasite helminths (81.77 % in *Larus maculipennis* and 88.89 % in *L. dominicanus* and *L. cirrocephalus* respectively). *Larus dominicanus* was parasitized by up to 6 different helminth species simultaneously, with higher percent of parasitism with 3 species (37.50 %). In *L. maculipennis* the highest percent of parasitism was found with a single species (47.62 %) and in *L. cirrocephalus* with one and two species (37.50 % in both cases) (Table I A). In all three species of studied seagull percent of parasitism found was higher for cestodes with similar values: 87.50 % in *L. dominicanus* and *L. cirrocephalus* and 85.71 % in *L. maculipennis* (Table I A).

Regarding prevalence estimates in *L. dominicanus* highest values corresponded to *Stephanoprora denticulata*, *Tetrabothrius argentinus* and *Alcataenia dominicana* (55.56 % in all three cases) (Fig. 1). In *L. maculipennis* and *L. cirrocephalus* the highest prevalence value was estimated for the cestode *P. porasa* (65.39 % and 55.56 %, respectively) (Fig. 1).

Highest mean intensity values were found for the nematode *P. argentata* (138) in *L. dominicanus* and for the digenean *T. fedtschenkoi* in *L. maculipennis* and *L. cirrocephalus* (56.43 and 24, respectively) (Fig. 2).

In *L. dominicanus* the nematode *P. argentata* (F=47.59 %) turned out to be the central species, the cestode *A. dominicana* (F=16.55 %) and the digenean *S. denticulata* (F=13.45 %) the secondary species, and 5 satellite species: *T. argentinus* (F=8.97 %), *Skrjabinoclava* sp. (F=6.21 %), *Microsomacanthus shetlandicus* Cielecka & Zdzitowiecki, 1981 (F=5.17 %), *Beaverostomum brachhyrhynchus* Gupta, 1963 (F=1.38 %) and *P. porosa* (F=0.69 %) (fig. 3). In *L. maculipennis*, the central species was the digenean (*T. fedtschenkoi*) (F=79.19 %), the secondary species the cestode *P. porosa* (F=14.43 %) and 6 satellite species: *Psilochasmus oxyurus* (Creplin, 1825) Lühe, 1909 (F=3.14 %), *Wardium paucispinosum* Labriola & Suriano, 2000 (F=1.60 %), *S. denticulata*, *T. argentinus* and *M. shetlandicus* (F=0.40, respectively) and *B. brachyrhynchus* (F=0.20 %) (Fig. 3). In

Table I. – A, Parasitism percentages in function of the helminth parasite species number for each group of host species. B, Fager affinity indices contingence tables. * Significant values with 5 % error.

Table I

A-

	L. dominicanus (n=9)	*L. maculipennis* (n=26)	*L. cirrocephalus* (n=9)	Total (n=44)
Without parasites	11,11%	19,23%	11,11%	15,91%
1 helminth species	12,50%	47,62%	37,50%	37,84%
2 helminth species	25%	33,33%	37,50%	32,43%
3 helminth species	37,50%	14,29%	25%	21,62%
4 helminth species	12,50%	0%	0%	2,70%
5 helminth species	0%	0%	0%	0%
6 helminth species	12,50%	0%	0%	2,70%

	L. dominicanus (n=8)	*L. maculipennis* (n=21)	*L. cirrocephalus* (n=8)	Total (n=37)
Parasitized with digeneans	62,50%	42,86%	50%	48,65%
Parasitized with cestodes	87,50%	85,71%	87,50%	86,49%
Parasitized with nematodes	12,50%	0%	0%	12,50%

B-

Larus dominicanus

	S.denticulata	*T. argentinus*	*P.porosa*	*A. dominicana*
S. denticulata	1	0.80*	0.67*	0.67*
T. argentinus		1	0.57*	0.44*
P. porosa			1	0.33
A. dominicana				1

Larus maculipennis

	S.denticulata	*T. argentinus*	*P. porosa*
S. denticulata	1	0	0.12*
T. argentinus		1	0.22
P.porosa			1

Larus cirrocephalus

	S.denticulata	*T. argentinus*	*P.porosa*	*A. dominicana*
S. denticulata	1	0	0.29	0.5
T. argentinus		1	0.67*	0
P. porosa			1	0
A. dominicana				1

* significant value with 5% error

L. cirrocephalus the *central species* was *T. fedtschenkoi* (F=68.57 %), the same as in the *L. maculipennis* helminthological community. *Secondary species* were represented by the cestode *P. porosa* (F=16.19 %) and by the digenean *S. denticulata* (F=10.48 %). *Satellite species* were *T. argentinus* (F=2.86 %) and *A. dominicana* (F=1,90 %) (Fig. 3).

In *L. dominicanus* the helminth with the higher abundance was *P. argentata* (15.33), while for *L. maculipennis* and *L. cirrocephalus* it was represented by *T. fedtschenkoi* (15.19 and 8, respectively) (Fig. 4).

Species richness of parasitic helminths present in all three gull species was 11 species: 8 in *L. dominicanus* and *L. maculipennis* and 5 in *L. cirrocephalus*. Helminth species common to all three communities were three: *S. denticulata*, *T. argentinus* and *P. porosa*. *B. brachyrhynchus* and *M. shetlandicus* were found in *L. dominicanus* and *L. maculipennis* but were absent in *L. cirrocephalus*. *A. dominicanus* was shared by *L. dominicanus* and *L. cirrocephalus*, and *T. fedtschenkoi* by *L. maculipennis* and *L. cirrocephalus*. *P. oxyurus* and *W. paucispinosum* were collected only in *L. maculipennis*; *P. argentata* and *Skrjabonoclava* sp. were only collected in *L. dominicanus*.

According to the Sorensen Similitude Coefficient obtained, the *L. dominicanus* and *L. maculipennis* communities were the most similar (62.50 %), followed by *L. dominicanus*-*L. cirrocephalus* and *L. maculipennis*-*L. cirrocephalus* (61.54 %) respectively. The Fager Indices values are shown in Table I B. For *L. dominicanus*, affinity indices were significative (=0.05) for all pairs of species, with the exception of *A. dominicana*-*A. argentina* (0.33). In *L. maculipennis*, the Fager Index was significative for the species pair *S. denticulata*-*T. argentinus* (0.12). For *L. cirrocephalus* the only significative value of the Fager index was *T. argentinus*-*A. argentinus* (0.67) (=0.05) (Table I B).

Regarding helminth species distribution along the gut in host species studied, *Psilochasmus oxyurus* was distributed in Duodenum II and Ileum I; *Stephanoprora denticulata* in Duodenum I, Ileum I, Ileum II and rectum and *Beaverostomum brachyrhynchus* was only present at Ileum II. *Tetrabothrius argentinus, Paricterotaenia porosa* and *Alcataenia dominicana* were distributed along all the gut. *M. shetlandicus* was found at Duodenum I, Duodenum II and Ileum I and *Wardium paucispinosum* was collected from Ileum I and II. (Fig. 5). With regard to *site shifting*, when *T. argentinus* is alone, it inhabits all the gut (genera-

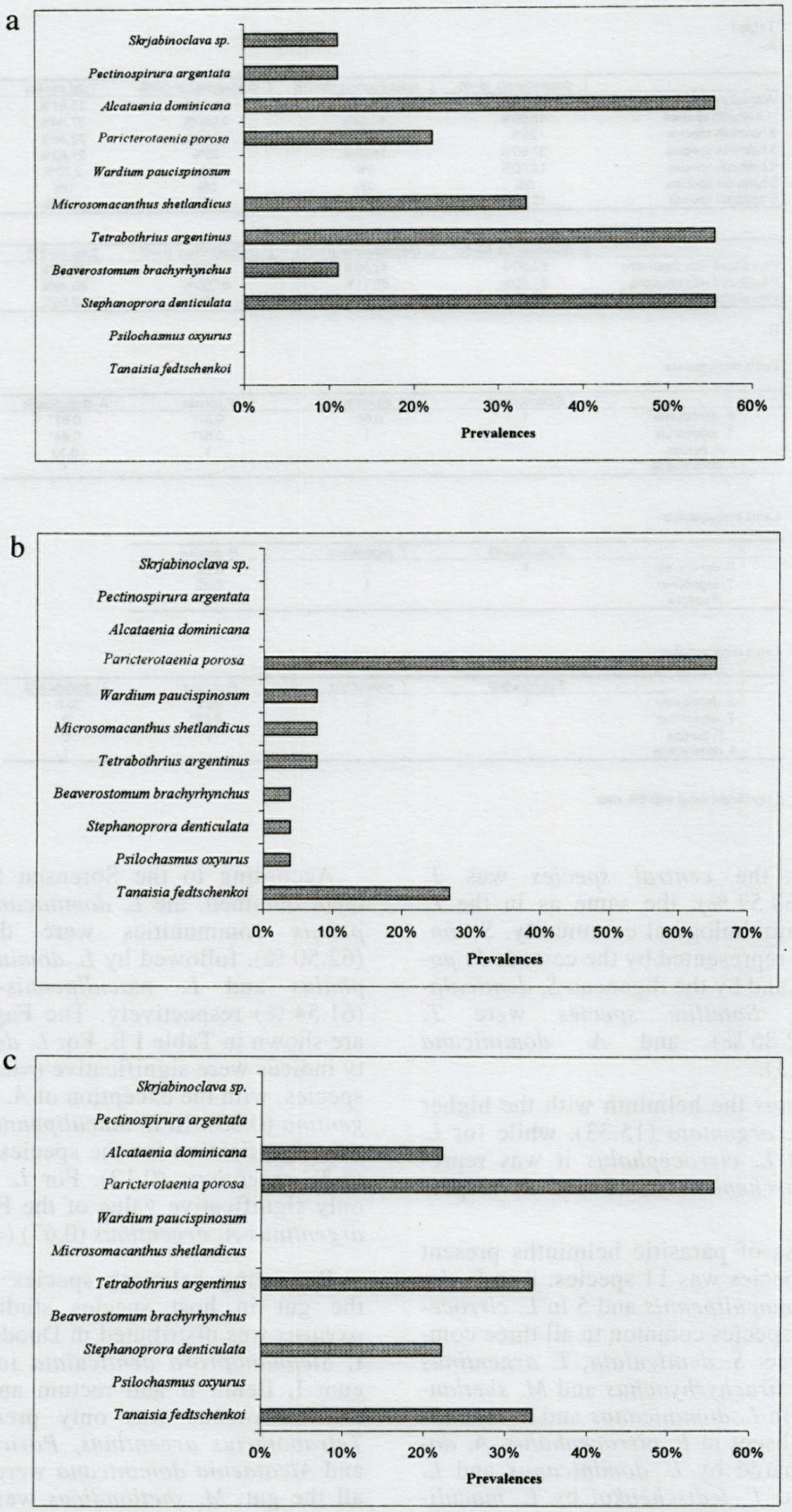

Fig. 1. – Parasite helminth prevalence in: a, *Larus dominicanus*; b, *L. maculipennis*; c, *L. cirrocephalus*.

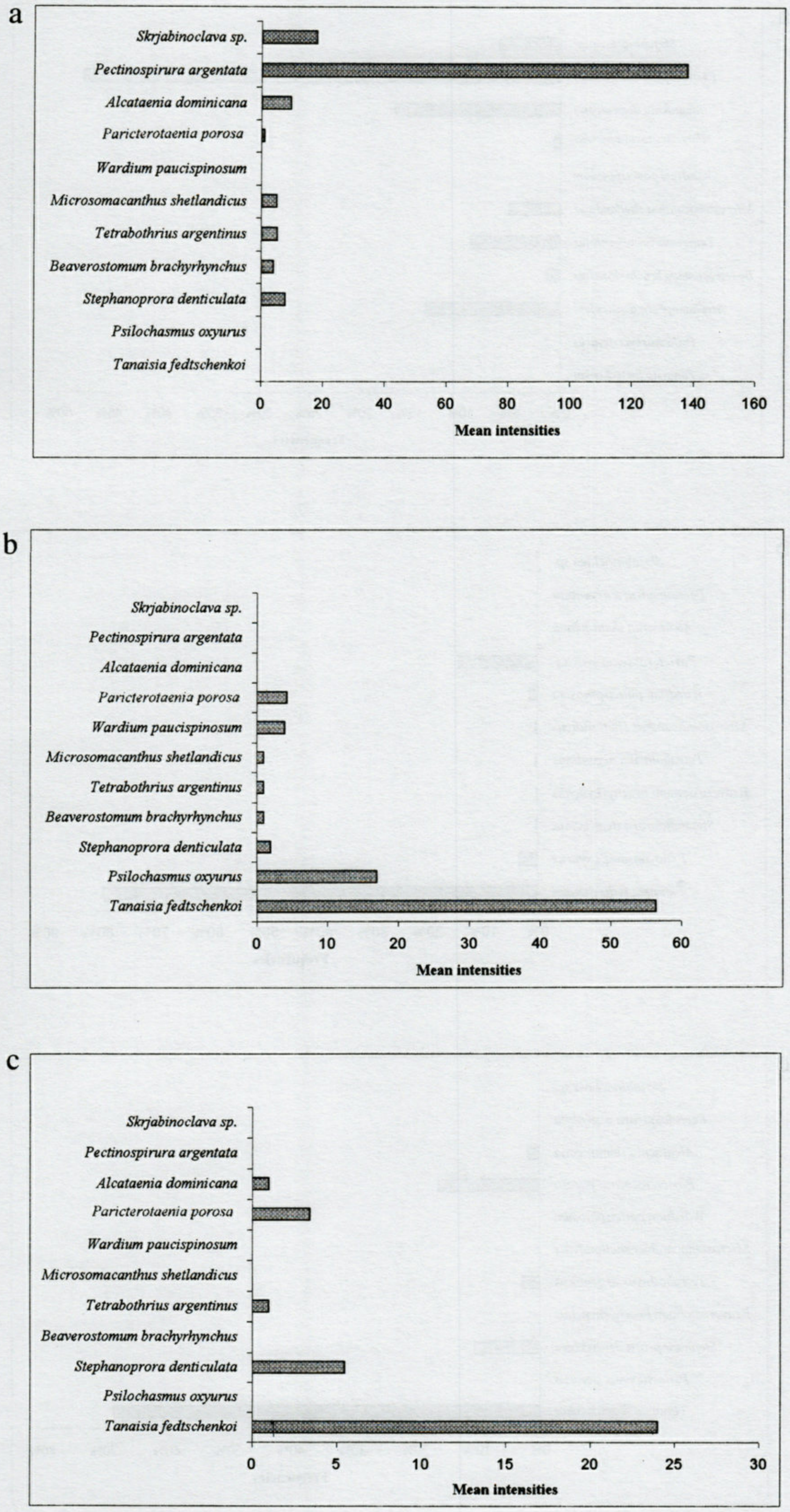

Fig. 2. – Parasite helminth mean intensities in: a, *Larus dominicanus;* b, *L. maculipennis;* c, *L. cirrocephalus.*

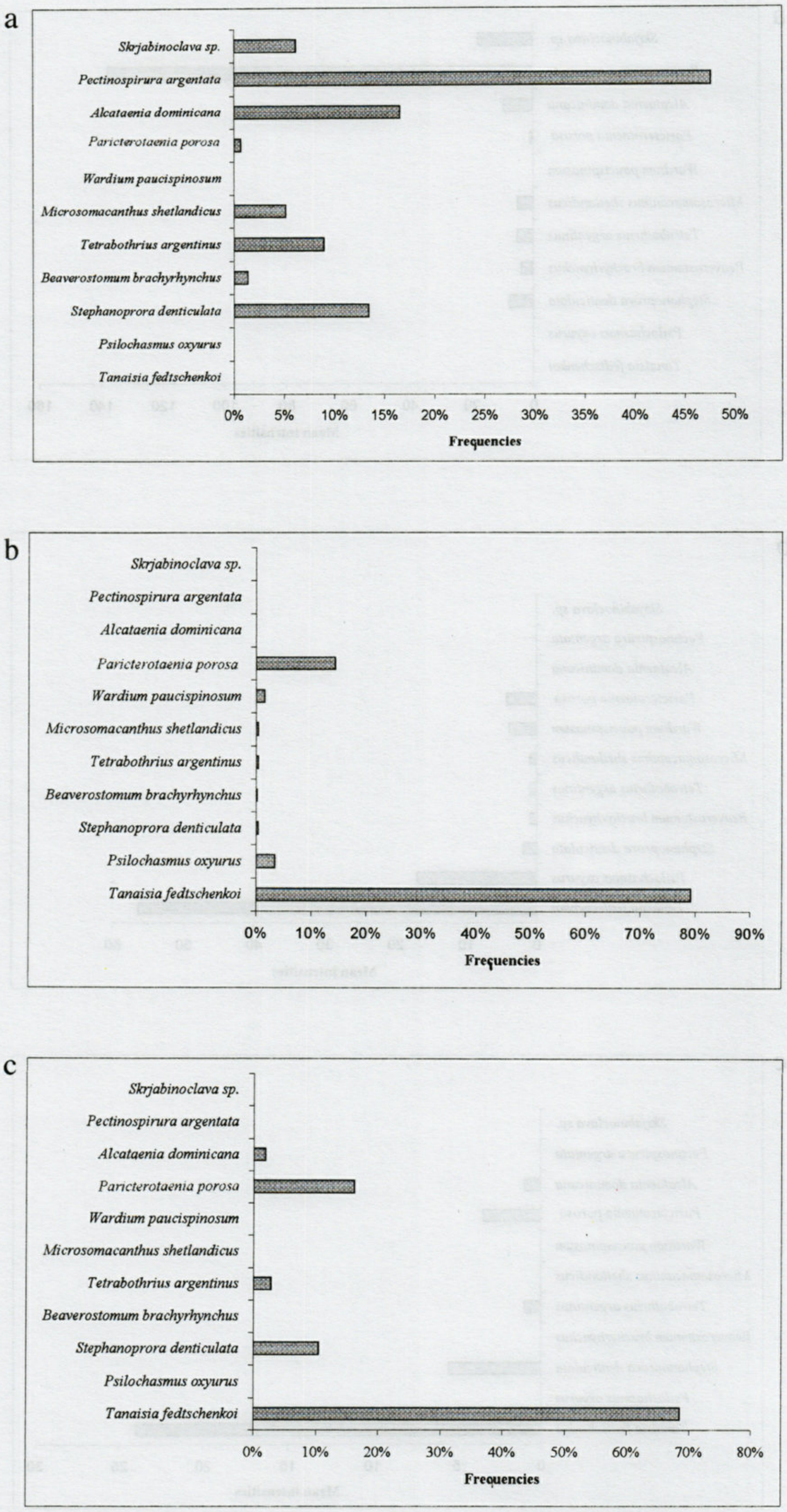

Fig. 3. – Parasite helminth frequencies in: a, *Larus dominicanus*; b, *L. maculipennis*; c, *L. cirrocephalus.*

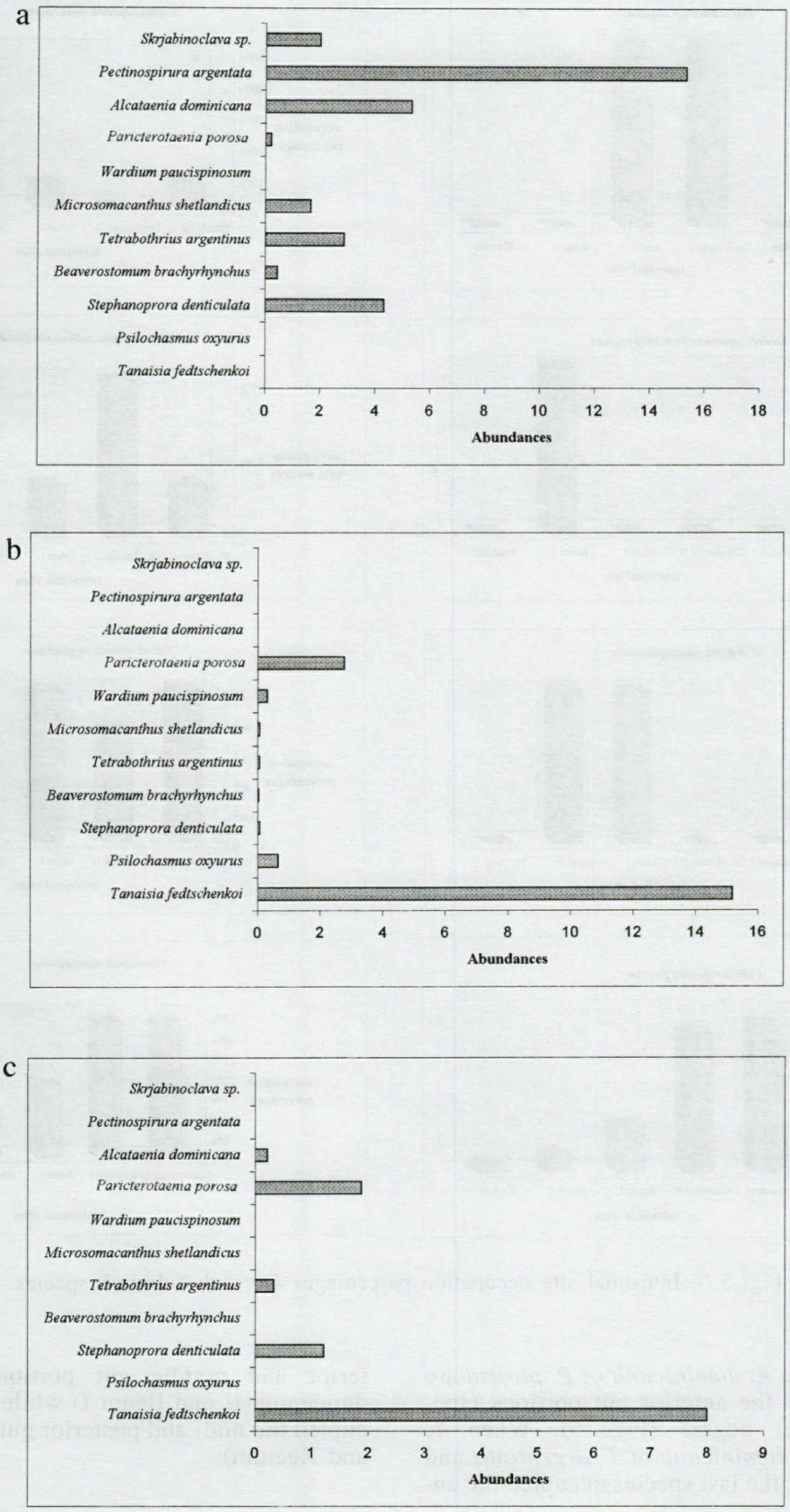

Fig. 4. – Parasite helminth abundances in: a, *Larus dominicanus*; b, *L. maculipennis*; c, *L. cirrocephalus*.

Figure 5

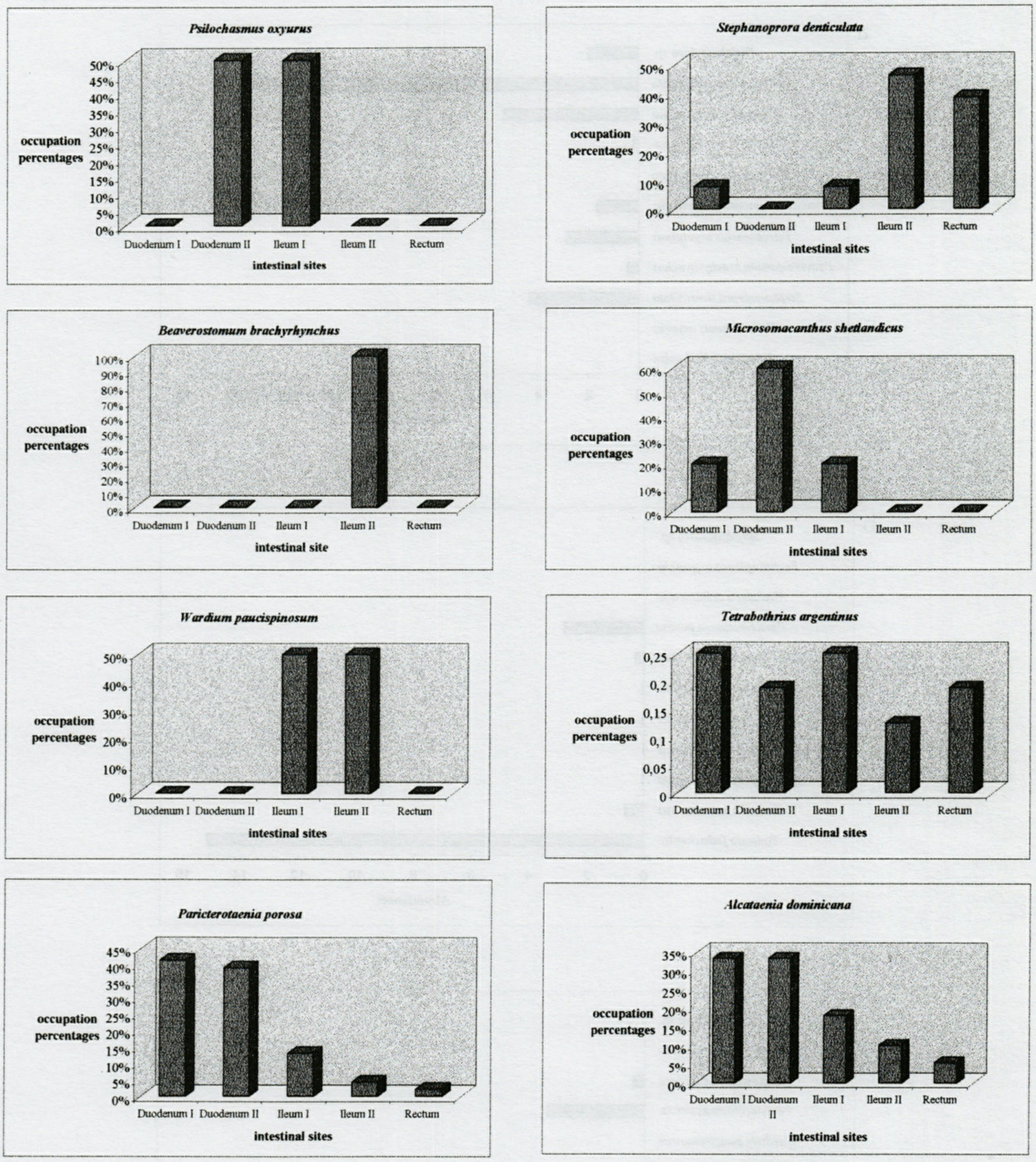

Fig. 5. – Intestinal site occupation percentages for each helminth species.

list) (Fig. 5). When *A. dominicana* or *P. porosa* are alone they occupy the anterior gut portions (specialists) in higher degree (Fig. 5). When *T. argentinus* and *A. dominicana* or *T. argentinus* and *P. porosa* cooccur, the last species occupied the anterior and middle gut portions (Duodenum I, duodenum II and Ileum I) while *T. argentinus* occupied the mid- and posterior gut (Ileum I, Ileum II and Rectum).

DISCUSSION

All three gull species considered have similar feeding habits, being associated in their feeding areas. However, it is necessary to take into account host feeding habits and areas and life cycles of their parasites to be able to explain the presence of the helminths found in each avian species and the composition of their helminthological community as well. This in turn allows inferring each bird's higher or lower association with marine, freshwater or terrestrial environment. With regard to digenean species found in all three communities as a whole, they were: *Tanaisia fedtschenkoi*, *Beaverostomum brachyrhynchus, Stephanoprora denticulata* and *Psilochasmus oxyurus*. Not all life cycles of all these species are known, but there are papers (Szidat 1957, Wisniewski 1958, Pojmanska *et al.* 1984), reporting that their intermediate hosts are freshwater gasteropods and that *S. denticulata* and probably *B. brachyrhynchus* have as secondary or paratenic host a freshwater fish. That indicates, in principle, that all three bird species caught freshwater prey. However, the structure of their respective helminthological communities (*T. fedtschenkoi* is the central species of the *L. maculipennis* and *L. cirrocephalus* helminthological communities but is not represented in *L. dominicanus* helminthological community, where the digenean *S. denticulata* is the secondary species) allows to infer that *L. dominicanus* eats preferentially fishes, while *L. cirrocephalus* and *L. maculipennis* eat mainly molluscs. Regarding the cestodes *Alcataenia dominicana*, *Paricterotaenia porosa, Wardium paucispinosum*, *Microsomacanthus shetlandicus* and *Tetrabothrius argentinus* are present in all three communities as a whole. Two common cestodes species were *T. argentinus* and *P. porosa. W. paucispinosum* was not present in *L. maculipennis*; *A. dominicana* in *L. cirrocephalus* and *W. paucispinosum* and *M. shetlandicus* in *L. cirrocephalus*. Although knowledge on life cycles of these cestodes is scarce, it is known that the life cycles of dilepidids involves a marine inshore crustacean as the only intermediate host (Jarecka *et al.* 1984, Galaktionov 1996, Hoberg 1996) while marine or freshwater copepods, ostracods or gammarids are the intermediate hosts of the majority of himenolepidid species parasites of aquatic birds. The tetrabothridean life cycle includes two intermediate hosts: a planktonic crustacean and a marine fish or cephalopod (Hoberg 1989, 1996, Galaktionov 1996). Nematode species present were *Pectinospirura argentata* and *Skrjabinoclava* sp. Although the life cycle of *P. argentata* has not been elucidated yet, nematodes of the Acuariidae family parasiting aquatic hosts develop in the hemocoel of marine crustaceans up to their third larval stage (Wong *et al.* 1989). Of all three gull species studied, only *L. dominicanus* was parasited by both aforementioned nematode species. All facts mentioned on life cycles of all helminths found apart from the table on parasite presence-absence suggest that though all host birds have similar feeding habits and their feeding areas sometimes overlap, *L. maculipennis* and *L. cirrocephalus* are preferably associated to the freshwater environments. On the other hand, in the community structure of *L. dominicanus* parasites, the central species (*P. argentata* and *Skrjabinoclava* sp) have a marine-related life cycle. On the other hand, digeneans whose life cycle involves freswater molluscs are absent from the aformentioned helminthological community. This suggests that *L. dominicanus* is the host species more closely associated to the marine environment and that, on the other hand, it feeds on larger prey than *L. maculipennis* and *L. cirrocephalus* (fishes and molluscs).

Two cases of site shifting were observed: that of *Tetrabothrius argentinus-P. porosa* and that of *T. argentinus-Alcataenia domincana*. In both cases *T. argentinus* shifted to the posterior gut portions in the presence of specimens from one of the two other species.

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DESCRIPTION OF *OWENIA GOMSONI* N. SP. (OWENIIDAE, ANNELIDA POLYCHAETA) FROM THE YELLOW SEA AND EVIDENCE THAT *OWENIA FUSIFORMIS* IS NOT A COSMOPOLITAN SPECIES

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POLYCHAETA
OWENIIDAE
NEW SPECIES
MORPHOLOGY
COMPLEX OF SPECIES

ABSTRACT. – Two *Owenia fusiformis* populations from different geographical locations were compared to assess whether this species has a truly cosmopolitan distribution. The specimens were collected in Gomso Bay (South Korean coast, Yellow Sea) and Banyuls Bay (south French coast, Mediterranean Sea). The comparison leads to the erection of the new species *Owenia gomsoni,* whose principal characteristics are: the presence of specific colour patterns on the branchial stems and body sides in living animals; a branchial plume mounted on a base with five pairs of lobes; a marked, laterally incised, collar-like fold at the boundary between branchial plume and thorax; teeth of the bidentate hooks vertically offset; very elongated setae scales and a marked preference for quartz grains during tube construction. The present observations on the new Yellow Sea species, complemented by others referred to in the paper, lead to a reduction in the distribution area of *Owenia fusiformis* Delle Chiaje. It is concluded that, in fact, the species is a complex. In consequence, it cannot be considered cosmopolitan.

POLYCHAETA
OWENIIDAE
NOUVELLE ESPÈCE
MORPHOLOGIE
COMPLEXE D'ESPÈCES

RÉSUMÉ. – Deux populations d'*Owenia fusiformis* d'origine géographique différente ont été comparées pour vérifier si la distribution de l'espèce est réellement cosmopolite. Les spécimens ont été récoltés en Baie de Gomso (côtes de la Corée du Sud, Mer Jaune) et en Baie de Banyuls (côtes françaises de Méditerranée). La comparaison a conduit à la définition d'une nouvelle espèce *Owenia gomsoni,* dont les principales caractéristiques sont: la présence, sur l'animal vivant, de taches colorées spécifiques disposées à la base des branchies et sur les parois latérales du corps; un panache branchial émergeant d'une base constituée de cinq paires de lobes; un collier prononcé, incisé latéralement, représentant un pli circulaire du tégument, disposé à la limite du panache branchial avec le thorax; les dents des crochets décalées verticalement; des écailles sétales très allongées; une préférence marquée pour les grains de quartz lors de la construction du tube. La définition de cette nouvelle espèce récoltée en Mer Jaune ainsi que d'autres observations, conduisent à réduire considérablement l'aire de distribution d'*Owenia fusiformis* delle Chiaje. En conclusion, cette espèce représente un complexe d'espèces et ne peut être considérée comme cosmopolite.

INTRODUCTION

Much of the current taxonomy of marine organisms dates back to the 19th century. Many older studies were based on limited phenotypic and geographic information, and it is questionable how adequately these earlier monographs summarise true biological diversity (Knowlton 1993, Klautau *et al* 1999). Among the Polychaeta, Chaetopteridae and Oweniidae illustrate the influence of the past: observations made with outdated means contributing to the definition of many cosmopolitan species. In the genus *Chaetopterus,* Hartman (1959) synonymised 25 species and since then it has been considered monotypic with one highly variable cosmopolitan species *Chaetopterus variopedatus* (Renier). However, recent observations (Petersen 1984) reveal that the genus is not monotypic and that *c.* 10 species occur in the North Atlantic and adjacent waters alone. In Oweniidae, the genus *Owenia* was for a long time considered monotypic

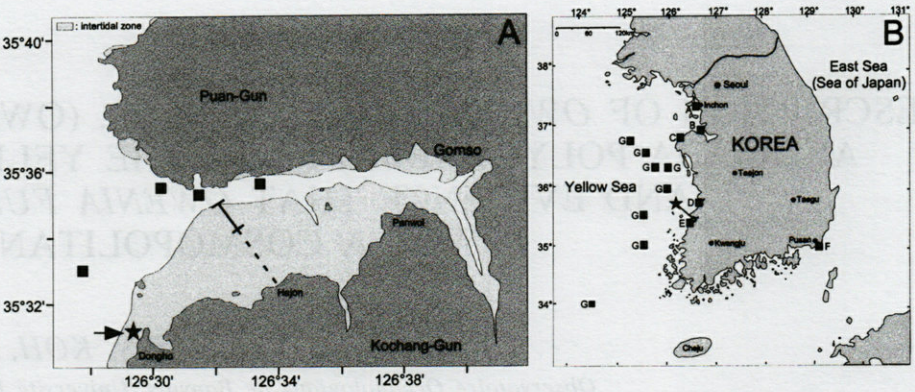

Fig. 1. – A, Map of the collection area of *Owenia gomsoni* n. sp. The asterisk indicates the type locality; four squares give the location of *O. gomsoni*; the straight line displays a radial of which the continuous part was positive for *Owenia*; data given by Pr Hong, Univ of Inha. B, Presence of *Owenia* sp, on the Korean coasts, from the following references: Lee CG 1999 (A); KORDI 1993 (B), 1994 (D), 1995 (C); KEPCO 1992 (E); Lee JH 1976 (F) and 1986 (G).

with only one species *Owenia fusiformis*. Despite many observations indicating morphological differences on specimens from widely separate areas (Caullery 1944, Hartman 1955, Thomassin & Picard 1972), and the erection of two new species, *Owenia caudisetosa* (Hartmann-Schröder 1959) and *O. collaris* (Hartman 1969), Dauvin & Thiébaut (1994) rejected these species and considered *O. fusiformis* to have a truly cosmopolitan distribution, with the exception of Antarctic waters. The absence of *O. fusiformis* from the Antarctic was in fact unjustified, since it had already been reported in the South Shetland Islands by Hartman-Schröder (1986) and more recently in the Ross Sea by Cantone & Sanfilippo (1992). Despite this worldwide distribution, the morphological differences linked to different geographical distributions led us to resume a meticulous morphological study based on individuals from widely separate biogeographical areas to assess whether *O. fusiformis* is truly a cosmopolitan species. Among Polychaeta, several species complex were already identified (Wilson Jr 1983, Hartley 1984, Williams 1984, Mackie & Pleijel 1995).

There are two possible approaches to the question of a homogeneous worldwide distribution of *Owenia fusiformis*. i) If we accept that a truly cosmopolitan species must maintain genetic cohesiveness mediated by gene flux throughout its distribution, a study of the larval dissemination from a perfectly identified source may either confirm or invalidate the reality of the gene flux. ii) The results of larval dissemination may be examined through the morphological divergences or similarities of widely separated benthic specimens. The first group of questions, concerning the true dissemination of larvae, was examined in several ways (Koh, in progress). For the present paper, we used only direct, classical methods in a morphological comparison between benthic material collected in the Yellow Sea and in the Mediterranean Sea. Representatives of both Mediterranean and Yellow Sea populations are tube-building polychaetes that commonly occur in dense assemblages in fine, muddy sand (Fager 1964, Dauvin & Gillet 1991, Somaschini 1993). The prostomium, fused to the achaetous buccal segment, has a frilled food-gathering membrane mounted on a polylobed base and surrounding the terminal mouth (Day 1967). The thoracic region comprises three short segments, each bearing only notopodia with capillary setae. Abdominal segments bear notopodial capillary setae and neuropodial hooks composed of a long shaft and two recurved teeth at the apex. The tubes project well above the surface of the sand in which they are embedded.

THE MATERIAL

The specimens used in the present study were collected at the type locality given by the asterisk in Fig. 1 (Latitude: 35°31 N; Longitude: 126°29'40 E) close to Dongho, in Gomso estuary, at low tide, 800 m from the shore. The maximum density (N.m^{-2}) for a patchy distribution was 12 specimens. The nature of the sediment, characterised by the parameter ∅, was medium sand (∅=1.77); by comparison, the Mediterranean sediment in Banyuls Bay was a fine sand (∅=2.6). The annual sea surface temperature range is from 0.5 °C to 28.5 °C (Park & Park 2000). *Owenia* has been reported in other parts of the Gomso estuary (Fig. 1A) and different sources also indicate its presence on the west and south coasts of South Korea (Fig. 1B). Lee J.H. (1976) used only the denomination *Owenia fusiformis*, as Paik (1989) in his Fauna of Korea. Part of the material (approximately 40 individuals) collected during the period 12-27 October 1999 was fixed with formaldehyde 5 %. The remainder (approximately 40 individuals) was transported alive from Korea to France. Specimens from the

Mediterranean Sea were collected in Banyuls Bay during the period 13-25 November 1999 using a van Veen grab, and kept alive in the laboratory. A pool of 14 individuals from the Yellow Sea and 20 from the Mediterranean Sea was used for measurements. The size of the animals varied with their origin; the total length of the body (mm ± sd) was 43.26 ± 2.95 and 23.05 ± 2.85 for the Yellow Sea and the Mediterranean specimens, respectively. Diameter (mm ± sd) at the level of the branchial-thoracic transition was 2.33 ± 0.30 and 0.99 ± 0.12 for the Yellow Sea and the Mediterranean specimens, respectively. The mean number of segments on whole individuals was 21.45 ± 2.30 (range from 16 to 24) and 16.6 ± 5.12 (range from 10 to 26) for Yellow Sea and Mediterranean Sea specimens, respectively. Similar-sized specimens were selected for morphological comparisons. Other specimens (approximately 280) were available from the collections of Pr Hong JS (Inha University) and Dr Lee JH (Kordi).

THE METHODS

The characters used until now to identify genera and species are macroscopic. From Fauchald (1977), the characteristics of the genus *Owenia* are as follows: the tubicolous animals are rather small, and often capable of moving around with the tube; prostomium is fused to the anterior segments and anteriorly protruded into a tentacular crown, ventrally entire. Five genera are defined: *Galathowenia*, *Owenia*, *Myriowenia*, *Myriochele*, *Myrioglobula*. Nilsen & Holthe (1985) report two of these genera, *Owenia* and *Myriochele*, in Arctic and Scandinavian areas, from the following features: head region with or without a tentacular crown, structure of the tube, presence of capillary and (or) acicular chaetae, presence of hooks on abdominal notopodia, tooth disposition on the hooks, number of ventral lobes on the pygidium. Cantone & Di Pietro (1998) erected a new species of *Myriochele* for the Antarctica province on the basis of macrocharacters: prostomium shape, presence of a slit on prostomium, collar size, pygidium lobes. In the present case, we identified new morphological criteria using both a dissecting microscope and a SEM. To extract the animals from their tubes, a circular incision was made in the median part of the tube and then the two ends of the tube were pulled in opposite directions. The specimens were anaesthetised with 8 % $MgCl_2$ for one hour to allow pictures to be taken. The Korean specimens were able to build a new tube when replaced in seawater after the effect of the anaesthetic had worn off. Specimens from the Mediterranean seemed more fragile and did not recover. Colour pictures where taken with a Leica-Wild MPS 32 through a Diaplan Leitz light microscope or a Wild M3Z compound microscope. Setae and hooks were dissected with a fragment of tegument on preserved specimens, rinsed three times in distilled water, 30 min each bath, run through a graded alcohol series and stored in 70 % ethanol until observation. Immediately before viewing in a Hitachi S.520 SEM (University of Perpignan, Centre of Electron Microscopy), they were transferred to 100 % alcohol, air-dried, attached to a stub and coated with gold palladium. Body fragments were critical-point-dried and then attached to the stub and coated.

SYSTEMATICS

FAMILY OWENIIDAE RIOJA 1917

OWENIA DELLE CHIAJE, 1844

Owenia gomsoni, new species

Etymology: the name reflects the collection area: the Bay of Gomso near the town of Kochang on the west coast of South Korea (Fig. 1).

Type material: Holotype: at the National Museum of Natural History (Paris) under the registered number MNHN-POLY 66 and paratypes (n=4) at the same museum under the registered number MNHN-POLY 67.

DESCRIPTION

The body may be divided into three sections: the branchial area or feeding organ, the thorax and the abdomen. A circular belt consisting of a pronounced furrow, or even a fold resembling a collar, separates the first two sections. The feeding organ has its base close to this collar; in consequence, branchial stems can be identified close to this collar (Fig. 2 A to C). On the mediodorsal surface, the area delimited by the first two lateral branchial stems is empty except near their bases, which are partially covered by a horizontally elongated unpaired and very flat lobe (Fig. 2A). On the medioventral surface, in the axial area anterior to the collar, a horizontal slit is clearly visible (Fig. 2B). The branchiae (Fig. 2C) are equal or subequal. Their constitution also varies. Out of 20 samples examined from the Korean coast, 13 had branchial plumes with 5 pairs (5 right + 5 left) of ramified stems and there were a few other very rare cases (Fig. 3).

The tegument of living specimens is sufficiently transparent to allow variously disposed red blood patches to be seen. Only on the thorax is the tegument a general greenish-brown colour. On this background, two white dorso-lateral bands start between setigers 1 and 2, reach their maximum width on setiger 2 and continue onto the first abdominal segment where they narrow as they become closer together. The same schema is found on the following abdominal segments. Three distinguishing characters on Korean specimens are i) They do not show the wine-coloured reddish patches found on the dorsal axis of the anterior region of the thorax and the branchial bases on Mediterranean samples. ii) Their branchial stems are delicately speckled with white. iii) Anterior to the furrow there are latero-ventral small ocular spots, most easily seen in the lateral view.

The thoracic region has three bundles of capillary setae (Fig. 4A). Under the dissecting microscope, these thoracic bundles are fair on Korean

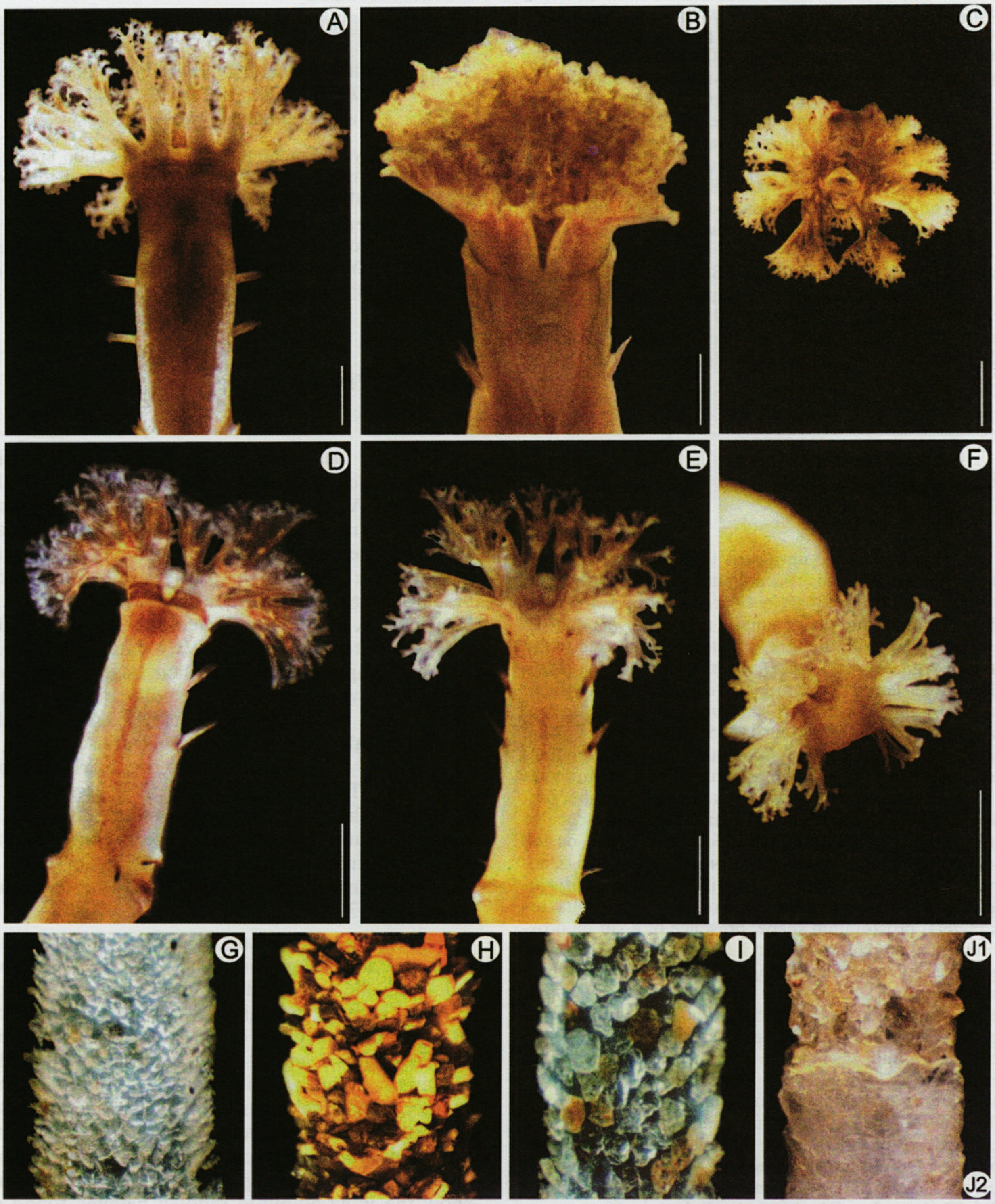

Fig. 2. – A to C: anterior part of a living specimen of *Owenia gomsoni*; A, dorsal view; B, ventral view; C, frontal view of the branchial plume. D to F: anterior part of a living specimen of *Owenia fusiformis*; D, dorsal view; E, ventral view; F, frontal view of the branchial plume. G to J, structure of the tube; G, tube built by *O. gomsoni* n.sp with natural sediment from the Yellow Sea (Bay of Gomso); H, tube built by *O. fusiformis* with natural sediment from the Mediterranean Sea (Bay of Banyuls); I, tube built by *O. gomsoni* n.sp with natural sediment from the Mediterranean Sea (Bay of Banyuls); J, two aspects of the same tube built by *Owenia gomsoni* n.sp; 1, part built in the Yellow Sea and 2, part built after transport to the Mediterranean Sea, each time with the locality's natural sediment, *i.e.* a sediment not selected by an experimenter. Scales: for A to F, 1 mm for each scale bar; for G to F, actual width of all tubes: 2.5 mm.

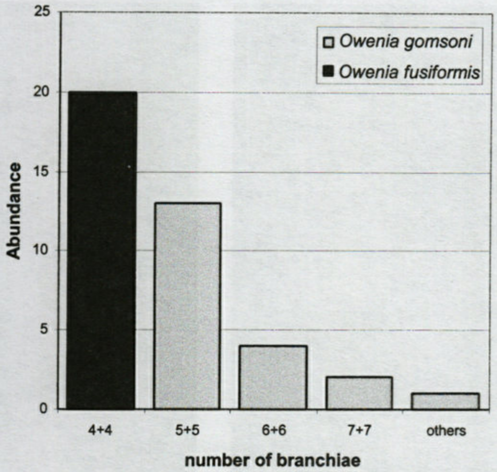

Fig. 3. – Variability in the constitution of the branchial plume for specimens from the two origins.

specimens. The abdominal region has biramous segments with notopodial capillary setae and minute neuropodial hooks with two curved teeth at the apex. These very numerous hooks are arranged in dense fields forming dorso-ventral tori covering 9/10 of the circumference of the body. On the larger specimens, there is a relatively small number (7 to 12) of hook rows on the first abdominal torus. In the tori, the hooks are arranged in regular rows with their teeth pointing forwards. The first torus is not different from the others. The abdominal part ends in a pygidium with no recognisable ventral lobes.

Observation with a SEM allowed us to describe hard structures (setae of the thoracic and abdominal parts, and abdominal hooks or uncini) in detail. Capillary setae (Fig. 5) covered in closely packed scales; they are not spinulous as described by several authors (Day 1967, Caullery 1944). This scaly cover is not total and leaves the seta's base quite smooth. The scales only begin to peel away from the shaft at the tip of the setae, giving an almost spiny appearance. Scales very slender, with a length/width ratio always over 3 (Fig. 5 A to C). Each uncinus has a long manubrium or shaft and its head carries two teeth arranged side by side (Fig. 6). In position on the body, the hooks point forwards. We adopt the convention that the forward direction of the hooks corresponds to their anterior or ventral face and that on an isolated uncinus it is possible to define a right and a left tooth. For rigorous comparison, the hooks were observed from three positions: side face, ventral face and apex face (Fig. 6 A to C). On a hook in a torus observed on the animal's left flank, the left tooth (furthest from the edge of the body) appeared longer when seen from the front of the animal and on the right flank it was the right tooth that appeared longer. The teeth are thus positioned symmetrically with respect to the longitudinal axial plane of the body. In addition, the longer tooth was also set in a lower position relative to the other; the offset of the upper part of the two teeth was observable in the side view of the hook and the offset of the end of the teeth was observable from an apex view. Three specific hook features are defined: regularly curved nuchal shape, rectilinear edge of the shaft head, and tooth offset.

COMPARISON WITH MEDITERRANEAN SPECIMENS

On Mediterranean specimens, the branchial ramifications are far from the thoracic collar, and this disposition leaves a broad circular area between the furrow and the first ramifications (Fig. 2D to F). The area delimited by the first two lateral branchial stems (Fig. 2D) is occupied by a protruding, in-

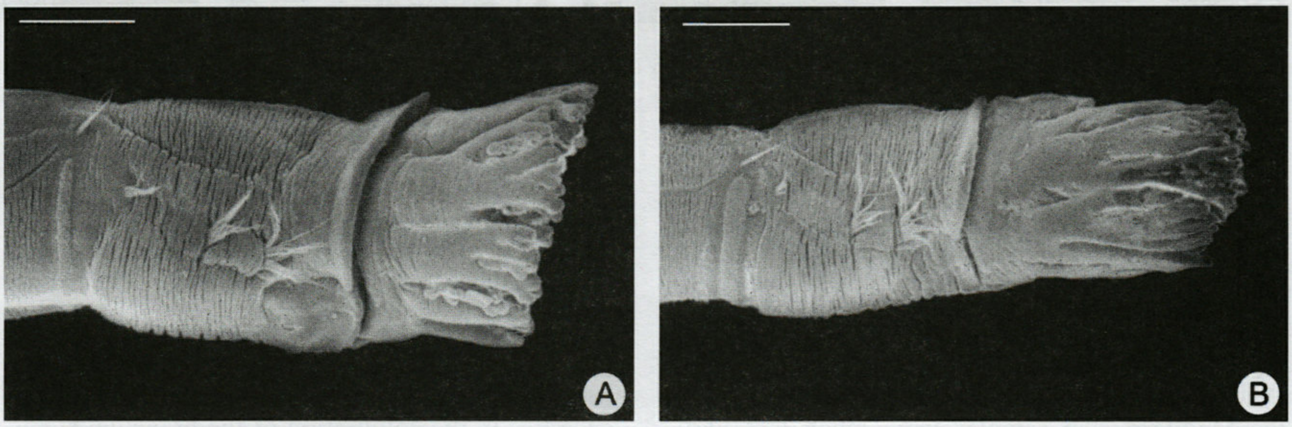

Fig. 4. – Thoracic part of the body of *Owenia gomsoni* (A) and *Owenia fusiformis* (B) observed with a SEM. The difference in width of tori on first abdominal segment in the two specimens is evident. Scale bars: 500 µm.

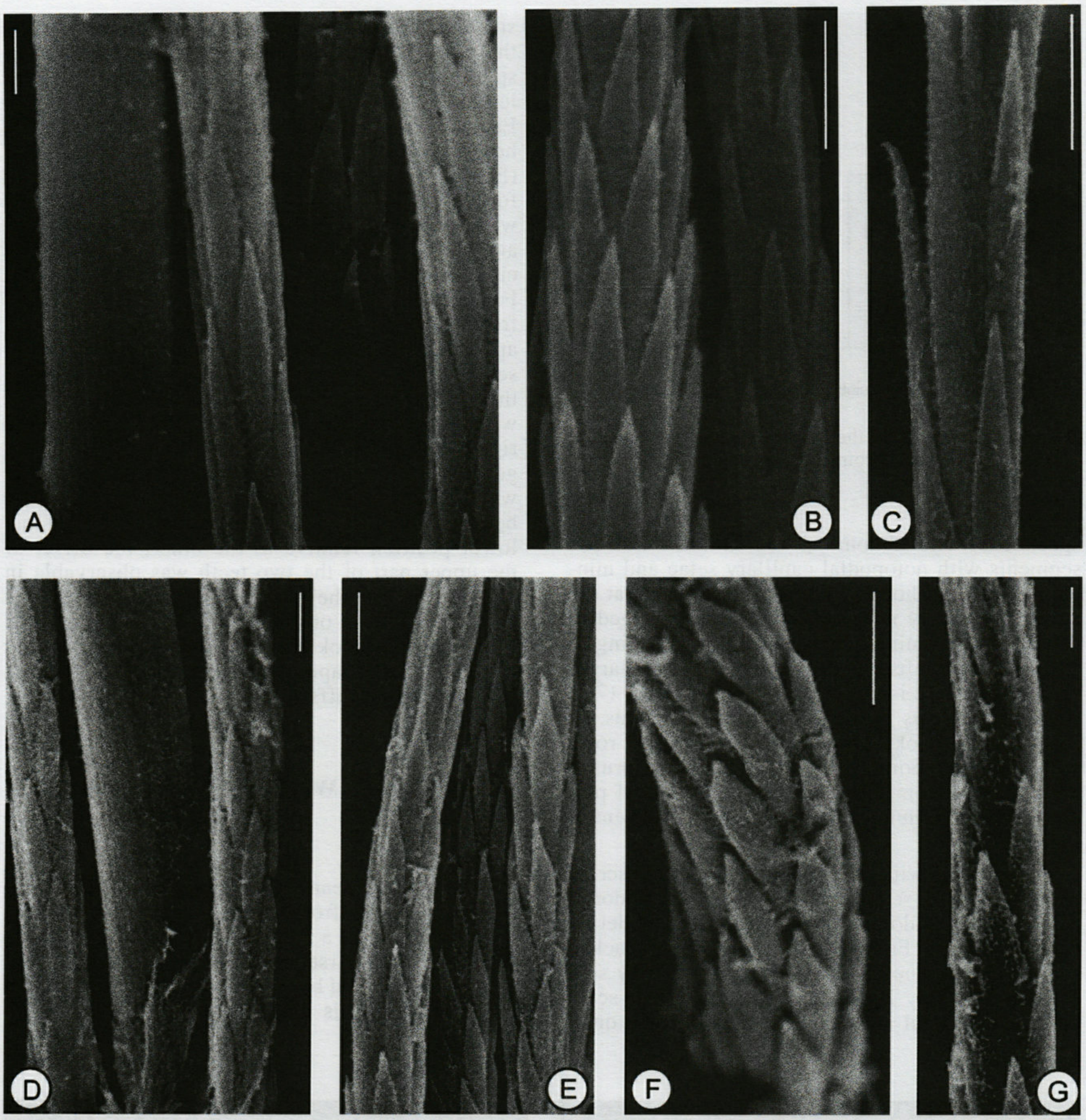

Fig. 5. – Comparative observation of hard structures with a SEM. Setae. A to C: setae on *Owenia gomsoni*; D to G: setae on *Owenia fusiformis*. Scale bars: 2 µm.

verted-V-shaped, unpaired lobe. On the medioventral surface, in the axial area anterior to the collar, the clear horizontal slit observed on Korean specimens (Fig. 2B) is absent on Mediterranean specimens (Fig. 2E). The branchiae increase progressively from the median ventral line to the median dorsal line (Fig. 2F). Their constitution also varies. Out of 20 samples examined (Fig. 3) the Mediterranean samples were much less variable: all 20 samples examined had 4 pairs of ramified stems.

The Mediterranean samples had a pale, transparent tegument, with the exception of the thorax, which was off-white to pale grey. The white dorsolateral bands present in the Korean specimens are not found on Mediterranean specimens. There is a wine-coloured reddish patch on the dorsal axis of the anterior region of the thorax and the branchial bases on Mediterranean samples. Another difference lies in the colouration of the branchial stems, which are delicately speckled with white on Korean specimens but not on Mediterranean speci-

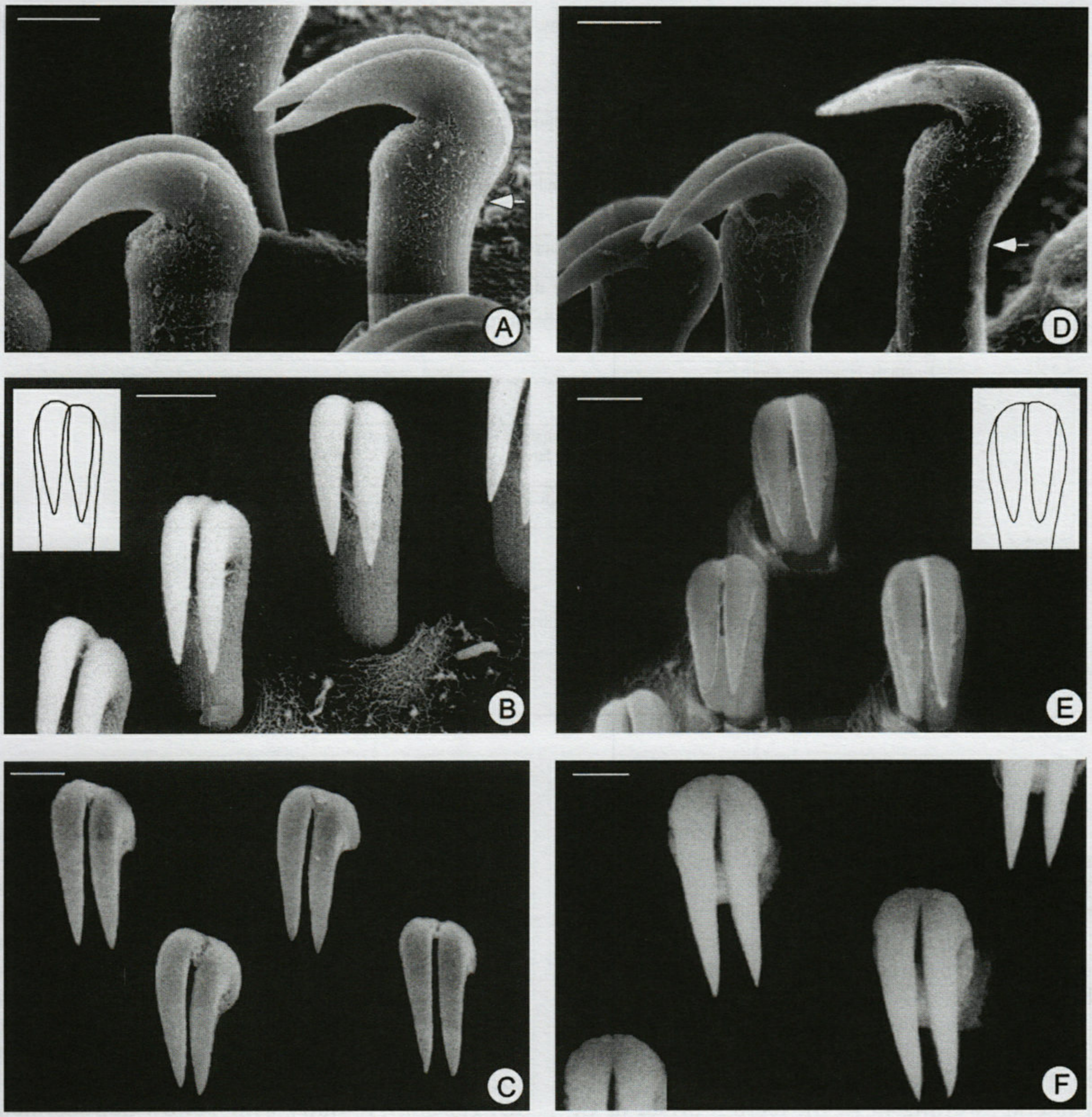

Fig. 6. – Comparative observation of hard structures with a SEM on specimens of both origins. Hooks. A to C: hooks of *Owenia gomsoni*; D to F: hooks of *Owenia fusiformis*. Three observation angles are given: side view (A and D), ventral view (B and E) and apical view (C and F). Scale bars: 2 µm.

mens. Anterior to the furrow there are latero-ventral ocular spots, larger than on Korean specimens.

The thoracic region has three bundles of capillary setae (Fig. 4B). Under the dissecting microscope, these thoracic bundles are not fair, as on Korean specimens, but black. The distance between these bundles is not the same on specimens from different origins. This point needs to be clarified in view of the size differences. If the position of each bundle is measured from the start and end of the thoracic section, the distance between bundles 1 and 3 is the same for both origins, but the position of this section is variable, as the part of the thorax it occupies is much further from the first abdominal segment on the Korean specimens.

The abdominal region has biramous segments with notopodial capillary setae and minute neuropodial hooks with two recurved teeth at the apex. The first torus is different from the others: it is raised up and surrounded by a wine-coloured margin. The number of rows of hooks on this first abdominal torus observed on smaller specimens from Mediterranean Sea was relatively high with 14 to 16 rows. A comparison with the Korean specimens leads to the conclusion that the number of rows was smaller on larger specimens (cf also Gambi 1989 Fig. 3A).

The SEM observation allowed us to identify differences in the setae of the thoracic and abdominal parts, and in the abdominal hooks or uncini.

Table I. – Comparison of *Owenia gomsoni*, from the Yellow Sea, with *Owenia fusiformis*, from the Mediterranean Sea, based on specimens of similar size.

Features	***Owenia gomsoni***	***Owenia fusiformis***
colour of the tube and selection of material	white or light brown: selection of silicious elements	dark brown: selection of carbonated elements
pigmentation of the body	two lateral white pigmented bands	red patches on the dorsal axis of the anterior part of the thorax and of the branchial bases
ocular spots	two small ocular spots disappearing after fixation	two large ocular spots still visible after fixation
insertion area of branchiae	first ramifications close to the thoracic border forming a collar	first ramifications far from the thoracic border forming a flat belt
number of branchial stems	predominance of 5 pairs	4 pairs
length of branchiae	short	long
number of dichotomies	few	many
inter branchial area on the medio-dorsal axis	with a horizontally flattened, unpaired lobe partially covering the two lateral branchial stems	with an unpaired lobe, raised in an inverted "V" between the two lateral branchial stems
median axis of the ventral thoracic part	presence of a clear horizontal slit	absence of relief or ornamentation or slit
collar at the thoracic border	with a lateral incision	short lateral incision
dorso-ventral offset of hook teeth	always present	absent or not frequent
macroscopic coloration of setae	off-white over the whole length of the body	black on the thoracic segments and on first abdominal segment
uncinal rows on torus of first abdominal segment	7-12	14-16

As stated above for Korean specimens, the shape of the scales differs depending on the origin of the material, and on Mediterranean specimens (Fig. 5D to G) they were relatively shorter, with a length/width ratio always below 3. In order to successfully link hook shape to geographic origin, standardised viewing positions were adopted. Between the Korean (Fig. 6A to C) and Mediterranean (Fig. 6D to F) samples, three differences may be identified: i: nuchal shape – regularly curved in A, angled in D; ii: shaft head – rectilinear edge in B, slight lateral swelling in E; iii: teeth – offset in C, not offset in F.

TUBE BUILDING EXPERIMENTS

The tubes of the Yellow Sea specimens (Fig. 2G) were characterised by their brilliant white colour due to the selection of grains of quartz, which are rare in their natural sediment, a dark grey sand. Consequently, the pale tubes were easily distinguishable on the sedimentary bottom. On the tubes of the Mediterranean Sea specimens, the sedimentary particles were inserted at random into the mucus by their face with the smallest surface area: they were thus perpendicular to the tube wall, which had many external asperities (Fig. 2H). When placed on the Mediterranean sediment from Banyuls Bay, Korean individuals built tubes with a larger variety of grains that gave an almost brown colour, but still with a predominance of quartz (Fig. 2I). On the same basic sediment, specimens from the Yellow Sea and the Mediterranean Sea did not select the same fraction. Yellow Sea worms selected clear grains of quartz. Mediterranean worms used a larger variety of material, principally carbonated grains. The grains were also assembled differently. On the tubes of the Yellow Sea specimens, the grains were arranged in lines following two diagonal directions and applied to the external wall of mucus by their widest face, so that they appeared to be slightly overlapping. The tube built by *O. gomsoni*, initially with Yellow Sea sediment and then, after transport, with Mediterranean sediment, is illustrated in Fig. 2 J1 and J2 (cf also Vovelle 1963 for tube building of *Owenia* from the French coast). From these two descriptions it is possible to build a comparative table which summarizes the main differences (Table I).

DISCUSSION

Although frequently reported around the Japanese coast (Imajima & Morita 1987 for review), *Owenia fusiformis* was only recently described for the first time on the Korean coast (area around Pusan), by Lee (1976), before being included in the Fauna of Korea by Paik (1989). From these descriptions, it is already possible to point out differences from European specimens. Imajima & Morita (1987) described *O. fusiformis* from Japanese waters with specific characteristics such as a low collar enclosing the tentacular bases with two short slits on the ventral side. A single slit is described in the present paper on Yellow Sea specimens but no slits are found on Mediterranean specimens. The available literature also contains many examples of geographical divergences bearing both on macroscopic features and on the shape of uncini. Hartman (1955: 46, pl. 2, Figs 6-7), from the presence of a membranous thoracic collar and hooks with long teeth, created a subspecies *Owenia fusiformis collaris*, which was later promoted to the level of a species *O. collaris* Hartman (1969 p 493). Thomassin & Picard (1972) reported a difference in the shape of the apex of hooks between specimens from the Mediterranean Sea (near Marseille) and those from the Indian Ocean (near Tuléar, south-west Madagascar) but did not suggest the existence of a new species. Fauchald (1977) recognised in the works of Thomassin and Picard (1972) the first observations obtained with the help of the SEM, which allowed the characterisation of hook shape (cf also Nilsen & Holthe 1985, Imajima & Morita 1987, Gambi 1989, Martin 1989, for the use of the SEM). From an ecological point of view, Caullery (1944) also announced the probable existence of different species in any two climatically distant areas. He said "I am convinced that no identity exists between individuals from cold polar waters and those inhabiting warm tropical waters. There are almost certainly divergences between them, at least physiological, that make them distinct races and there are perhaps also morphological divergences, but very difficult to identify". Finally, Uschakov (1971) did not list *Owenia fusiformis* among the amphipacific species of polychaetes. This resistance in the face of clear morphological and ecological evidence is probably due partly to the widespread opinion that there are no biogeographical regions for polychaetes (Fauvel 1959) and partly to the important role assigned to the planktonic larval stage in the establishment of the gene flux. Wilson (1932) described the larval phase in the life cycle of Oweniidae and estimated the length of its larval life at four weeks. Scheltema (1986, 1989) emphasised that larval transport was the main source of gene flow. But from the moment that decoupling was evident between the presence of a planktonic larva in the life cycle and the size of the specific area (Bhaud 1998 a and b), the morphological divergences previously observed acquired a new significance. In addition two direct reasons: i) the small likelihood that a gene flux could act on the scale of the whole world and ii) the limited planktonic larval dispersion observed in the Mediterranean Sea, favoured the acceptance of a limited gene flux. In other words, the stimulation of and progress in systematics arises primarily from ecological considerations. If a more thorough morphological investigation followed by the erection of a new species is the logical consequence of these observations, the new species will not necessarily lead to the suppression of the cosmopolitan character of *Owenia fusiformis*. Several species may cohabit. However, in the present case, the new species will not be juxtaposed with *O. fusiformis* but will take its place and consequently the area of *O. fusiformis* will be reduced. Each time a difference is identified that justifies the erection of a new species, *O. fusiformis* will lose its cosmopolitan character still further. For instance, we are now in a position to announce that the differences in the morphology of hooks on specimens from the Indian Ocean, the Atlantic Ocean and the Mediterranean Sea are, in our considered opinion, sufficient to justify the erection of a new species in each of these areas (work in progress).

In conclusion, the geographical extension of *Owenia fusiformis* delle Chiaje seems smaller than has been accepted until now. Its range is progressively restricted (Myers & de Grave 2000). A detailed examination of the morphology of individuals accepted as belonging to this species, and their comparison with specimens from *terra typica* (Mediterranean Sea), lead to a negative response to the question posed by Dauvin and Thiébaut (1994): Is *Owenia fusiformis* delle Chiaje a cosmopolitan species ?

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REMARK. – The present work is not only the description of a new species but also an element of a larger programme to verify the reality of species with a cosmopolitan distribution, to define the role of large-scale larval dissemination and to identify the spatial limits of successful recruitment. Two programmes were involved in this work: European INTAS97-0916 under the leadership of D Martin, Blanes, Spain and the French National Programme on coastal environment: PNEC (ART2).

Note added on proof. After presentation of this manuscript to the editor, we were aware of the work of Blake (2000) who reported for the Californian coasts two distinct species: the first was referred to Hartman's *O. collaris*; the second species was new to science and described as *O. johnsoni*. This work strongly corroborates our opinion that *O. fusiformis* is a species complex.

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PRYMNESIUM FAVEOLATUM SP. NOV. (PRYMNESIOPHYCEAE), A NEW TOXIC SPECIES FROM THE MEDITERRANEAN SEA

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PRYMNESIUM FAVEOLATUM SP. NOV.
PRYMNESIOPHYCEAE
SCALES
ULTRASTRUCTURE
TOXICITY
MEDITERRANEAN

ABSTRACT. – A new marine species of *Prymnesium* is described based on cultured material originating from a sublittoral sample collected on the eastern French Mediterranean coast. *Prymnesium faveolatum* sp. nov. exhibits typical generic characters in terms of cell morphometry, swimming mode and organelle arrangement. Organic body scales, present in several proximal layers, have a narrow inflexed rim and are ornamented with a variably developed cross. Scales in the single distal layer have an upright peripheral rim and an alveolate pattern of ridges. This new species appears to be widely distributed in the Mediterranean Sea. On the basis of scale ornamentation, two groups are recognized within those *Prymnesium* species described by electron microscopy, a separation hypothesized to be related to ploidy level. Preliminary toxicity tests indicate that *P. faveolatum* is a toxic species.

PRYMNESIUM FAVEOLATUM SP. NOV.
PRYMNESIOPHYCEAE
ECAILLES
ULTRASTRUCTURE
TOXICITÉ
MÉDITERRANÉE

Résumé. – Une nouvelle espèce marine de *Prymnesium* est décrite à partir d'une souche provenant d'un prélèvement réalisé dans la zone supralittorale sur la côte est méditerranéenne française. *Prymnesium faveolatum* sp. nov. présente les caractères du genre en ce qui concerne la forme des cellules, la nage et la disposition des différents organites. Des écailles organiques formant plusieurs couches proximales ont une marge étroite et sont ornementées d'une croix dont les extrémités sont plus ou moins ramifiées. Les écailles distales, en une seule couche, ont un bord vertical périphérique et sont ornées d'alvéoles. Cette nouvelle espèce semble bien répartie dans la Méditerranée. En se basant sur l'ornementation des écailles, il est possible de discerner deux groupes parmi les différentes espèces de *Prymnesium* étudiées au microscope électronique; l'hypothèse d'une séparation en relation avec la ploïdie est émise. Les résultats préliminaires des tests de toxicité indiquent que *P. faveolatum* est une espèce toxique.

INTRODUCTION

The genus *Prymnesium* Massart ex Conrad (Prymnesiophyceae, Haptophyta) is characterized by cells possessing two flagella, a short, non-coiling haptonema, and at least two types of organic scales covering the cell. Intensive interest in this genus has been provoked by the realisation from 1920 onwards that some of its members are the toxic agents responsible for reported fish kills in diverse regions of the world (see reviews by Moestrup 1994, Edvardsen & Paasche 1998, and references therein).

Since different species of *Prymnesium* are practically impossible to distinguish under the light microscope (LM), their identification requires, as is often the case with other haptophytes such as members of the closely related genus *Chrysochromulina* Lackey, transmission electron microscope (TEM) examination of the ornamentation of the organic scales covering the cell. Several authors have recognized the difficulty of confidently designating organisms to species originally described on the basis of LM observations only (Green *et al.* 1982, Billard 1983, Chang & Ryan 1985, Pienaar & Birkhead 1994). At present, only 6 species of *Prymnesium* have been unambiguously described through TEM studies. The first, *P. parvum* N. Carter (Manton & Leedale 1963), was followed nearly 20 years later by *P. patelliferum* Green, Hibberd et Pienaar (as *Prymnesium patellifera*, Green, Hibberd & Pienaar 1982), which has subsequently been shown by flow cytometric analysis to be in fact the alternating haploid phase of *P. parvum* (Larsen & Edvardsen 1998, Larsen 1999). Soon afterwards 3 new species were described: *P. annuliferum* Billard and *P. zebrinum* Billard (Billard 1983) and *P. calathiferum* Chang et Ryan (Chang & Ryan 1985). The last new species to be discovered, some 10 years later, was the unusual *P. nemamethecum* Pienaar et Birkhead (Pienaar & Birkhead 1994). Excellent schematic summaries of the ornamentation of the scales of these different species are provided by Moestrup & Thomsen (1995) and Larsen (1998).

While the distal scales of each of these species has a different, and hence characteristic pattern, *P. nemamethecum* is the only one in which the proximal (body) scales also possess a specific ornamentation. In this paper we present a new species of *Prymnesium* characterized by the ornamentation of its distal scales, but also, like *P. nemamethecum*, by the pattern of its proximal scales. This new species, isolated from a sublittoral water sample collected on the French "Côte d'Azur", seems to be widely distributed in the Mediterranean Sea.

MATERIALS AND METHODS

The culture examined in this study (Algobank strain HAP79) originated from a single cell isolation from a water sample collected on the 1st May 1996 from the intertidal zone at the beach of Roquebrune Cap Martin on the eastern French Mediterranean coast and subsequently enriched with 50 % Es-TrisII medium (Cosson 1987). Two further strains are maintained in the Algobank collection: Hap79bis was isolated from a sample collected at the same locality shortly afterwards, and Hap79ter isolated by Chrétiennot-Dinet & Puigserver from a sample collected on 23rd June 1998 at 24 m water depth in the bay of Banyuls (western French Mediterranean coast). The cultures are maintained in Es-TrisII medium at ambient temperature with natural illumination from a north facing window.

Living and fixed cells were observed with a Leitz Orthoplan optical microscope equipped with differential interference contrast optics (DIC). For whole mounts, a cell suspension, after brief exposure to osmium tetroxide vapours, was mounted on 0.5 % formvar coated copper grids, rinsed, and negatively stained with 1 % aqueous uranyl acetate or shadowcasted with gold-palladium. For sectioned material the technique employed was a slight variation of that of Green *et al.* (1982). 9 ml of culture were fixed with 1ml of 25 % glutaraldehyde solution for 1.5 hours. Cells were rinsed 3 times in culture medium using gentle centrifugation and post-fixed in 2 % osmium tetroxide in 0.1M sodium cacodylate (pH 7.2) overnight. After rinsing in the same buffer solution, the pellet of cells was pre-embedded in 0.2 % purified agar, dehydrated through a graded ethanol series and embedded in Spurr's low viscosity resin. Sections, cut with a diamond knife, were double stained for 30 minutes in 2.5 % uranyl acetate in 50 % ethanol, followed by 10 minutes in Reynold's lead citrate. All preparations were examined using either a Siemens 1A or Siemens 102 TEM.

Preliminary toxicity tests were conducted using *Artemia salina* Leach nauplii, the standard reference animal for such tests, following the protocol of the ARC test of the University of Ghent, Belgium. Five 48 h old nauplii were placed in an Eppendorf tube containing 1.5 ml of dense culture of the strain to be tested. Six replicate tubes were inoculated and the experiment conducted twice, giving a test with a total of 60 *Artemia* for each algal species. The mortality of *Artemia* nauplii was visually determined after 24 h of exposure to the algae in the dark. *P. parvum* (Algobank strain Hap45, isolated in 1977 by Billard), a toxic species well known to be the causative agent of fish kills, was used as the positive control species, and *Isochrysis galbana* Parke (Algobank strain Hap34, origin Plymouth collection, 1973) as the negative control. A further control in sterile sea water medium was also conducted.

OBSERVATIONS

Diagnosis

Prymnesium faveolatum sp. nov. Fresnel

Cellulae natantes elongatae vel elongatissimae (8-9 µm × 4-5 µm), parte postica acuminata et parte antica leviter oblique truncata. Appendices, in depressione subapicale insertae. Flagella duo heterodynamica et subaequalia (16-14 µm) ad apices attenuata. Haptonema breve et spiram non formans (2-2.3 µm). Cellulae duarum formarum squamarum tectae. Pluristrata squamae corporis proximales, ellipticae vel ovales (0.38-0.41 µm × 0.28-0.30 µm) cum cristis radiantibus in quattuor quadrantes in aspectu distali et proximali visibilibus (circa 15 per quadrantem); superficies distalis planum, angustum inflatum marginem et ornamentum secondarium cruciforme plus minusve ramiforme limite quadrantium habens. Stratum distale unicum, squamas ellipticas (0.30-0.36 µm × 0.25-0.27 µm) cum cristis radiantibus in quadrantes (circa 15 per quadrantem) in aspectu distali et proximali visibilibus, superficies distalis margine verticale (0.07-0.08 µm alte) et ornamento secondario faveolato cum ramis lateralibus labro conjunctibus. Chloroplasti duo fulvi parietales per longitudinem cellulae quisque pyrenoide lentiforme immersa. Nucleus centralis inter chloroplastos, corpus Golgi parabasale. Vacuola pluries in parte postica prominens. Corpuscula mucifera peripherica. Modus natandi celeriter, cellulis circum axem longitudinem revolventibus.

Motile cells elongate to very elongate (8-9 µm × 4-5 µm), posteriorly tapered, anteriorly slightly obliquely truncated. Appendages subapically inserted. Two subequal heterodynamic flagella (14-16 µm) terminating in a hair tip. Short, non-coiling haptonema (2-2.3 µm). Cells covered by two types of scales. Several layers of proximal body scales, elliptical to oval (0.38-0.41 µm × 0.28-0.30 µm) with a radial fibrillar pattern in quadrants (about 15 lines per quadrant) on both faces, and on the distal face a narrow inflexed rim, and a central thickening forming a variably pronounced 'X' shape along the intersection of the quadrants. The single outer layer consists of elliptical scales (0.30-0.36 µm × 0.25-0.27 µm) with a pattern of radiating fibrils in quadrants (about 15 lines per quadrant) on both

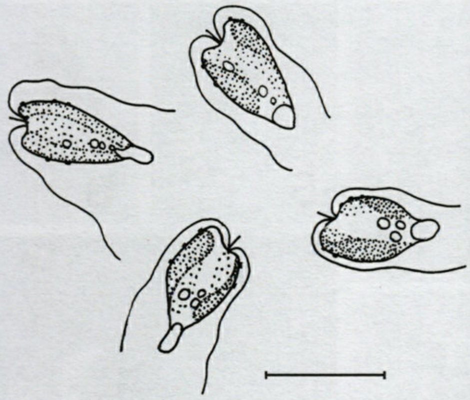

Fig. 1. – *Prymnesium faveolatum* sp. nov.; different aspects of living cells. Scale bar = 10 µm.

faces, the distal face also with a peripheral upright wall (0.07-0.08 µm high) and secondary raised alveolate ornamentation with side branches joining the rim. Two yellowish brown parietal chloroplasts, each with an immersed lenticular pyrenoid, lie along almost the entire length of the cell. Other cell contents include a median nucleus which lies in between the chloroplasts, and a parabasal Golgi body. A vacuole often prominent in the posterior part of the cell. Peripheral muciferous bodies present. Swimming motion rapid, spiralling around the long axis of the cell.

Holotype: Figures 9-17.

Origin: Sublittoral zone, Roquebrune Cap Martin, near Monaco on the French Mediterranean coast. Type material collected in 1996. Type strain: Hap79 in the Algobank collection at the University of Caen.

Etymology: Latin *faveolutus*, *-a*, *-um*, adj. meaning finely honeycombed, reflecting the precise character of the ornamentation of the distal scales.

Light Microscopy

Compared with other *Prymnesium* species, *P. faveolatum* grows extremely rapidly under our culture conditions; shortly after subculturing into fresh medium the cells aggregate into yellowish brown patches at the surface of the liquid and at the walls of the culture flask, and within days form a dense yellowish brown suspension throughout the medium. Observed at low magnification in the LM, cells exhibit a strong tendency to clump together (Fig. 2). Their very elongated, posteriorly tapered shape (Fig. 1) can clearly be seen at low magnification (Fig. 3) as at higher magnifications (Fig. 4, 7). Cells stressed after several minutes viewing under a coverslip usually become more rounded, and in old cultures cells may be spherical and often settle to the bottom of the culture flask, but remain motile (Fig. 6, 8).

Active cells of *P. faveolatum* swim very rapidly, spiralling around their long axis. Cells usually swim straight, but stop and change direction often. Sometimes cells are observed turning in tight circles. In normal swimming, the flagellar pole faces the direction of movement and the flagella trail backward along the sides of the cell (Fig. 5, 6). When, on rare occasions, the cells are observed swimming with the flagellar pole facing backward, the heterodynamic nature of flagellar movement is clearly seen; one flagellum undulates slowly, while the other beats rapidly, propulsing the cell forwards. Cells possess 2 large parietal yellowish brown to golden brown chloroplasts. A vacuole is situated in the posterior region of the cell along with droplets of reserve metabolite. In young cultures with active cells, the chloroplasts are often separated at the flagellar pole and the vacuole and metabolite droplets form a posterior prolongation to the cell (Fig. 4, 7). In older cultures, the numerous accumulations of reserves are brightly birefringent.

Normal elongated cells typically measure 8-9 × 4-5 µm. The two subequal flagella, 14-16 µm in length, and the short, non-coiling haptonema, measuring only 2-2.3 µm, are subapically inserted in an anterior groove. The ratio of flagellar length to cell length is 1.76. Encysted stages have never been observed in this species.

Electron microscopy

In TEM whole mounts, the hair tip of each flagellum and the short, non-coiling haptonema are clearly observed (Fig. 9). The scales covering the cell are of two types (Fig. 10-17). The proximal (body) scales, present in several layers, are elliptical to oval (0.38-0.41 × 0.28-0.30 µm) with a radial fibrillar pattern in quadrants (ca. 15 lines per quadrant) on both faces, and on the distal face a narrow inflexed rim (Fig. 11) and a central thickening forming an elongated "X" shape along the intersection of the quadrants (Fig. 14-16). Most often simple (Fig. 14), this central ornamentation shows considerable variability in form between scales. The points of the "X" may each be extended into two or three branches (Fig. 15), and the branches from two different points may occasionally join up to form irregular circles (Fig. 16). While not possessing a differentiated haptonematal scale as such (i.e. with a different pattern as in *P. nemamethecum*, Pienaar & Birkhead 1994), the body scales of *P. faveolatum* are typically smaller (0.30 × 0.18 µm) in the region of the flagellar insertion than on the rest of the cell (Fig. 10 and 19). Scales in the single outer layer are elliptical (0.30-0.36 × 0.25-0.27 µm) with a pattern of radiating microfibrils in quadrants on both faces (Fig. 10), the distal face also with a peripheral upright wall (0.07-0.08 µm high) which collapses in specimens viewed flat on a grid, but can clearly be seen in sections (Fig. 12), and secondary raised alveolate

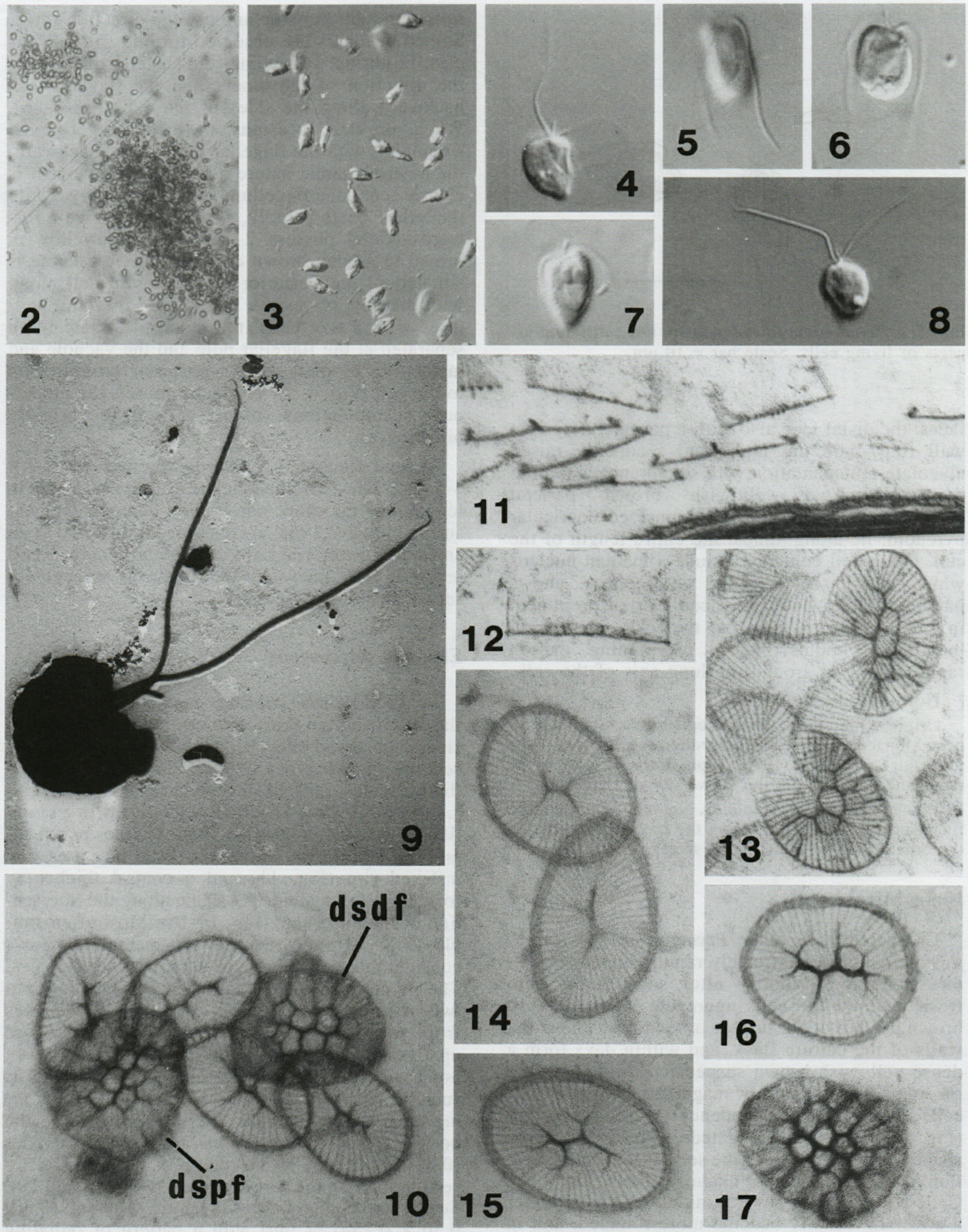

Fig. 2-17. – *Prymnesium faveolatum* sp. nov. 2-8, Light micrographs: 2, cells aggregating (× 160); 3, elongated shape of cells (× 400); 4-8, detail of living cells (× 1600). 9-17, transmission electron micrographs: 9, shadowcast (Gold/Palladium) of whole cell showing detail of flagella and haptonema (× 4400); 10-17, all × 84000: 10, 14-17 negative stained, 11-13 sections; 10, group of scales: two distal scales showing distal face (dsdf) and proximal face (dspf), and small body scales from the haptonematal region; 11-12, cross sections of two scale types; 13, tangential section of scales; 14-16, body scales showing increasing complexity of central thickening; 17, distal scale distal face with alveolate ridges and collapsed rim.

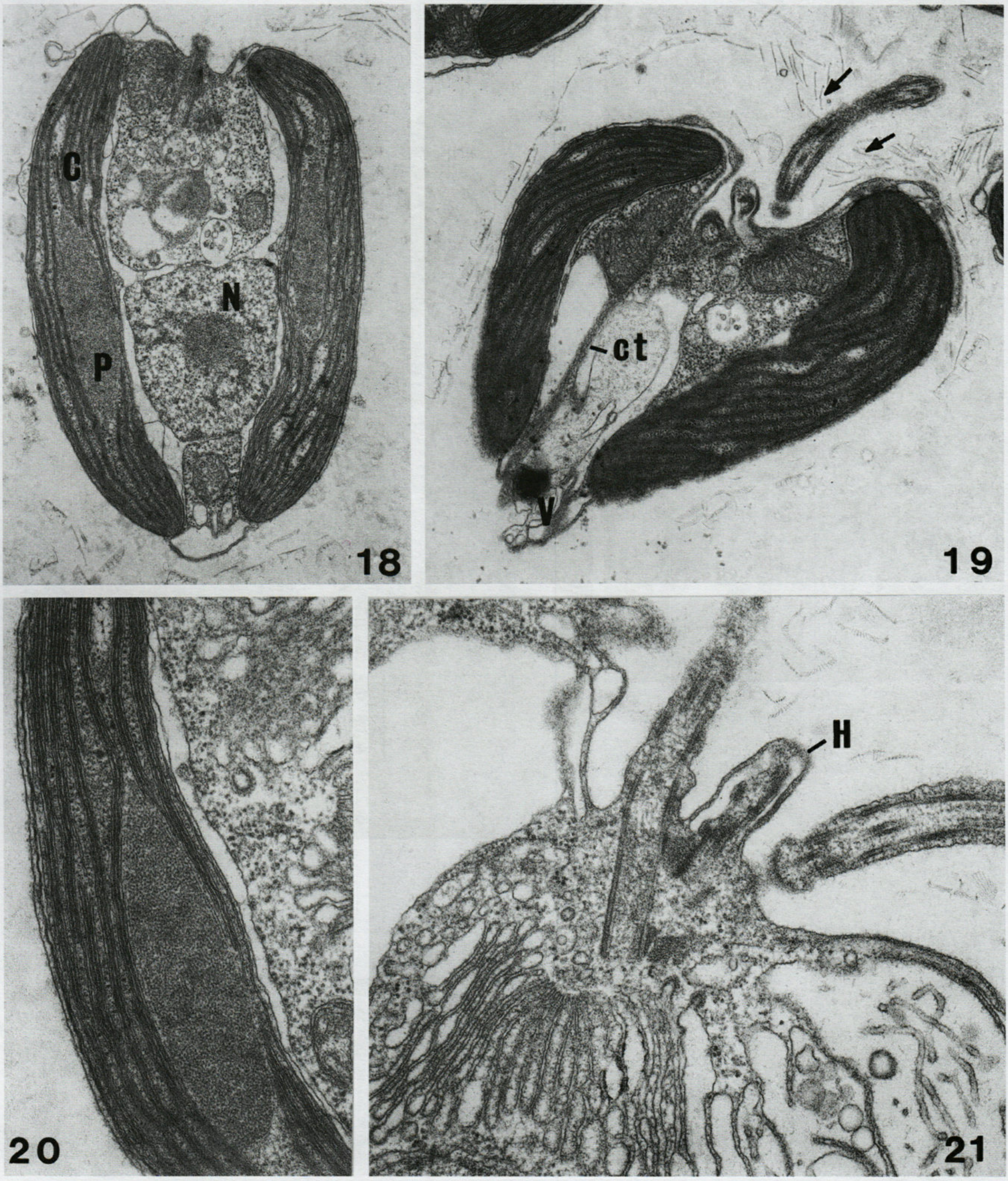

Fig. 18-21. – *Prymnesium faveolatum* sp. nov. 18, longitudinal section of whole cell showing the nucleo-plastidial complex: median nucleus (N) and two parietal chloroplasts (C) with immersed pyrenoid (P)(× 15500); 19, oblique section showing flagellar apparatus in apical groove with several layers of small scales (arrows) surrounding emergent flagella, posterior vacuole (V). Note the cytoplasmic tongue (ct) which extends through the cell (× 15500); 20, detail of immersed pyrenoid (× 42000); 21, section of apical zone showing Golgi body surrounding the flagellar bases, and emergent haptonema (H) (× 38000).

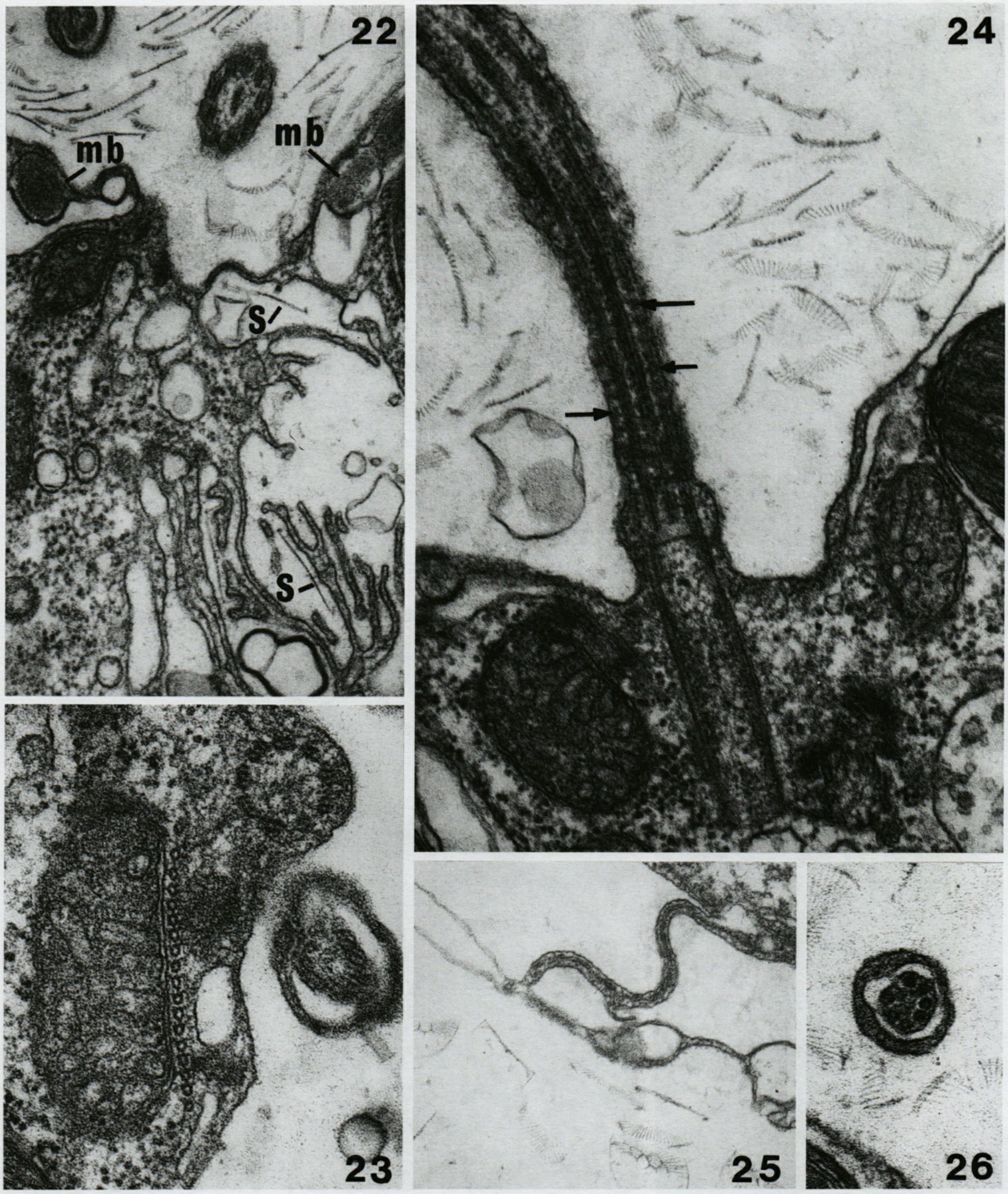

Fig. 22-26. – *Prymnesium faveolatum* sp. nov. 22, Forming scales (S) in Golgi vesicles in the region of flagellar insertion, and two muciferous bodies (mb) (× 47000); 23, cross section of sheet of microtubules of root 1 passing over the surface of a mitochondrion (× 65000); 24, longitudinal section of a flagellum showing tubular rings under the flagellar membrane (arrows), above the transitional region (× 58800); 25, part of the cytoplasmic tongue attached to the plasma membrane (× 42000); 26, cross section of emergent haptonema showing 7 microtubules surrounded by a sheath of the endoplasmic reticulum (× 82000).

ornamentation with side branches joining the rim (Fig. 17). This honeycomb pattern of the distal scales is the main distinguishing feature of the species and is the derivative of its name.

Thin sections reveal ultrastructural features typical of the Haptophyta and very similar to that of other *Prymnesium* species (Manton & Leedale 1963, Green *et al.* 1982, Billard 1983, Chang & Ryan 1985). The two chloroplasts each contain an immersed lenticular pyrenoid (Fig. 18, 20) in which fragments of traversing thylakoids are occasionally observed. The chloroplast membrane is continuous with that of the median nucleus (Fig. 18), the cell also containing numerous mitochondrial profiles. The Golgi body, which possesses intercalary dilations typical of haptophytes, is polarized around the flagellar bases (Fig. 21). Scales are formed in Golgi cisternae and released in the region of the flagellar insertion (Fig. 22). Few muciferous bodies are present under the surface of the cell membrane (Fig. 22). The flagella and haptonema emerge from an anterior subapical groove (Fig. 19, 21). The flagellar root 1 (R1) is simple, consisting of a sheet of ca. 18 microtubules which pass over the surface of a mitochondrial profile (Fig. 23), with no associated crystalline root. A continuation of this root, the cytoplasmic tongue (Gayral & Fresnel 1983), extends deep into the cell (Fig. 19), emerging far from the flagellar bases where it may be observed in contact with the plasma membrane (Fig. 25). In longitudinal sections of flagella, tubular rings are observed above the transitional region between the outer doublets and the flagellar membrane (Fig. 24), as described by Birkhead & Pienaar (1994). The emergent haptonema consists of 7 microtubules surrounded by a sheath of endoplasmic reticulum (Fig. 26).

Toxicity test

The mortality rates of *Artemia* (60 nauplii) after 24 h exposure to cultures of the different microalgal species were: 96.6 % for *P. parvum* (positive control), 75 % for *P. faveolatum*, 3.3 % for *I. galbana* (negative control), and 0 % in medium only.

Geographic distribution

First seen in a sample from the coast of Malta in 1986 (collected by JFs mother), then in 1987 from the Island of Spetsae in eastern Greece (collected by P. Griveau, friend). Observed for the first time at Roquebrune Cap Martin, France in 1989 (mixed with *P. zebrinum*) and the type culture isolated from a sample from the same location taken in 1996. Subsequently identified in samples from the bay of Banyuls, France in 1998 (by M.-J. Chrétiennot-Dinet), and from Blanes, northeastern Spain, also in 1998 and in 2000. *P. faveolatum* is thus found in diverse regions of the Mediterranean Sea. Having had the opportunity to collect sea water samples several times each year since 1980 at Roquebrune Cap Martin, it is noteworthy that after the first observation of this species at this locality in 1989, it has systematically been present only since 1996. *P. calathiferum* and *Prymnesium* sp. (=Algobank strain Hap53) are common in this part of the Mediterranean, and infrequently we have also observed *P. zebrinum* and *P. annuliferum*. Our observations of *P. faveolatum* over the last 15 years suggest a progressive westward spreading of this species in the Mediterranean (Aegean Sea/ French coast/Spanish coast).

DISCUSSION

This new species clearly belongs to the genus *Prymnesium*, the generic characters easily discernible under both the LM (cell shape, short and non-coiling haptonema, swimming mode, and absence of a dominant non-motile life stage) and EM (general arrangement and fine structure of organelles). The ornamentation of the distal scales of *P. faveolatum*, finely alveolated on their distal face, characterizes this new species, and is sufficient to differentiate it from the 6 other species described by TEM studies. The ornamentation of both proximal and distal scales of *P. faveolatum* is schematically summarized in Fig. 27. Of the species described before the advent of electron microscopy, cell size and shape distinguish *P. faveolatum* from the much smaller *P. minutum* N. Carter and the continental species *P. czosnowskii* (Czosnowski) Starmach, the latter also being globose (Green *et al.* 1982). Differences from the remaining (and type) species, *P. saltans* Massart ex Conrad, are less clear, the swimming mode providing the most obvious distinguishing character, that of *P. saltans* having been described as typically erratic and jerky with flagella extended obliquely forward (Conrad 1941, Heynig 1978). In addition, the haptonema of *P. faveolatum* is apparently markedly shorter than that of *P. saltans*, and the latter species has been reported from brackish waters, whereas *P. faveolatum* is in our experience exclusively marine.

Although *P. faveolatum* can be considered a typical *Prymnesium* species in terms of possessing only two types of organic scales compared to *P. nemamethecum* which has three types, it resembles the latter species in that these are the only two *Prymnesium* species described to date which have a specific pattern on the body proximal scales as well as the distal scales. In this respect, it is worth noting that while this body scale pattern is typically significantly different between these two species,

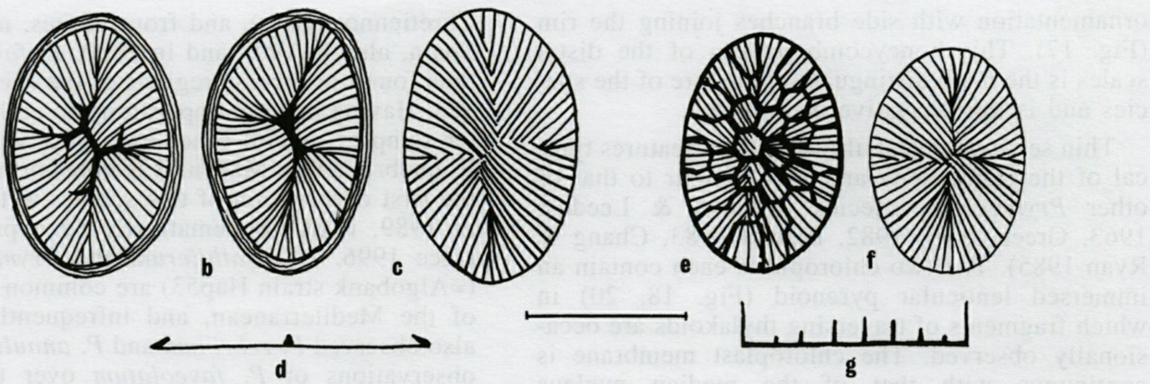

Fig. 27. – *Prymnesium faveolatum* sp. nov. Schematic drawing of scale ornamentation: (a-d) proximal (body) scales: (a,b) varying ornamentation of distal face (c) proximal face (d) transverse section showing narrow inflexed rim and central thickening. (e-g) distal scales: (e) distal face showing alveolate pattern (f) proximal face (g) transverse section showing upright peripheral rim and ridges of alveolate ornamentation. Scale bar = 0.25 µm.

the more complex crosses of *P. faveolatum* (this character shows considerable variability in both species) do resemble the simplest pattern in *P. nemamethecum* (compare our Fig. 15 with Fig. 15 in Pienaar & Birkhead 1994). The number of microfibrils per quadrant is, however, lower on both proximal and distal scales in *P. faveolatum* compared with *P. nemamethecum* (ca. 15 compared with ca. 30 respectively). These two species also differ in an important ultrastructural feature; the R1 of *P. faveolatum*, like that of *P. patelliferum* (Green & Hori 1990) is simple, while that of *P. nemamethecum* has an associated crystalline root (Birkhead & Pienaar 1994).

With the addition of this new species, two groups of *Prymnesium* can clearly be defined in terms of body scale ornamentation: (1) species having body scales with very narrow rims and radiating microfibrils on both faces; (2) species having body scales with a relatively wide inflexed rim, radial microfibrils on the proximal face, but also with a pattern of concentric ridges on the distal face (see schematic drawings of Larsen 1998). The first group includes *P. patelliferum* (=*P. parvum*, *patelliferum* stage), *P. nemamethecum*, and *P. faveolatum* (the latter two species also having secondary ornamentation on the distal surface of body scales). The second group comprises *P. parvum*, *P. annuliferum*, *P. zebrinum*, and *P. calathiferum*.

The pattern of the body scales of members of the closely related genus *Platychrysis* Geitler also fit into these groups, with *P. pigra* Geitler (Chrétiennot 1973) and *P. pienaarii* Gayral et Fresnel being the *P. parvum* type (group 2) and *P. simplex* Gayral et Fresnel the *P. patelliferum* type (group 1) (Gayral & Fresnel 1983). We have suspected for some time a digenetic cycle involving the latter two *Platychrysis* species, and the demonstration of such a cycle with *P. parvum* alternating with, and diploid relative to, the haploid *P. patelliferum* (Larsen 1999), obviously lends direct support to this idea. Further evidence comes from the body scale ornamentation of two further new *Prymnesium* species isolated from Mediterranean waters (Fresnel *et al.* in prep.). It seems very plausible that, as hypothesized for the coccolithophores (Fresnel 1994), scale ornamentation may be an indicator of ploidy level. We predict that *P. faveolatum* may thus eventually be joined in a life cycle with another group 2 (diploid) species.

In our experience the appearance of cysts in *Prymnesium* remains mysterious. Over several decades we have observed this phenomenon only twice; in *P. nemamethecum*, in which these stages were not reported by Pienaar & Birkhead (1994), and in Algobank strain Hap64, *Prymnesium* sp. In each case, the cysts appeared only briefly and on one occasion only. We have not seen cysts in cultures of other *Prymnesium* species, not even *P. patelliferum*, where these stages have been reported, but may be enhanced by higher salinities (Green *et al.* 1982).

Molecular genetic analyses of the small subunit 18SrRNA gene of a limited number of species within the family Prymnesiaceae indicate that *Chrysochromulina* is a polyphyletic genus, one sub-group forming a clade with *Prymnesium*, separate from another sub-group (Edvardsen *et al.* 2000). Detailed ultrastructural studies, including particularly reconstructions of the flagellar root system, have been undertaken for only relatively few members of this family, e.g. *Chrysochromulina apheles* Moestrup et Thomsen (Moestrup & Thomsen 1986); *C. scutellum* Eikrem et Moestrup (Eikrem & Moestrup 1998); *C. ahrengotii* M. Ø. Jensen et Moestrup (Jensen & Moestrup 1999); *P. patelliferum* (Green & Hori 1990), *P. nemamethecum* (Birkhead & Pienaar 1994). Since we currently maintain cultures of all described *Prymnesium* species except *P. nemamethecum* (our culture was lost, but this species was examined in detail by Birkhead & Pienaar 1994), as well as certain undescribed *Prymnesium* and all three described *Platychrysis* species, further molecular genetic and detailed ultrastructural examinations seem worthwhile in order to attempt to elucidate phylogenetic relationships within this group.

Toxicity tests previously carried out in our laboratory on cultures of various *Prymnesium* species (Lhuissier, Poncet unpubl results) have shown that the slow growing *P. zebrinum* is toxic to *Artemia*, while *P. annuliferum*, which grows very rapidly and produces dense cultures, shows no signs of toxicity. *P. faveolatum* is also a toxic species, the level of toxicity in our tests being somewhat lower than that of *P. parvum*, a species which has been reported on several occasions to be responsible for fish kills (see review by Edvardsen & Paasche 1998). To our knowledge, *P. faveolatum* has not been linked with any natural toxic events.

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