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Annales
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(A. S. B. L.)

Tome cent huit

Issue comprising the papers presented
at the First Workshop on the Systematics
of Marine Free-living Nematodes,
Gent, 13-16 August 1977

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FIRST WORKSHOP ON THE SYSTEMATICS OF MARINE FREE-LIVING NEMATODES

Gent, 13-16 August 1977

by

A. Coomans, L. De Coninck and C. Heip

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THE SYSTEMATIC POSITION OF THE FAMILY IRONIDAE AND ITS RELATION TO THE DORYLAIMIDA

by

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ABSTRACT

A critical review is made of the similarities and differences existing between the Ironidae and the Dorylaimida. The most important diagnostic features of the main groups of Dorylaimida, up to the superfamily level, and of the Enoplidae are listed. The family Ironidae is subdivided into two subfamilies of which the Coniliinae constitute a new subfamily with *Conilia* Gerlach, 1956 as the type genus.

From the detailed comparison of both groups it is concluded that the differences are important and that the similarities are probably the result of parallel evolution, occurring in two branches that evolved independently from a remote enoplid ancestor.

It is further argued that Ironidae do not fit well in Tripyloidea and are at present better included in Enoploidea.

On several occasions the similarities between *Ironidae* and *Dorylaimida* have been stressed, the extreme being the inclusion of the genera of the *Ironidae* in the family *Dorylaimidae* (Wieser, 1953). *Ironidae* are now usually classified under *Tripyloidea* in the *Enoplida*, but a close relationship between *Ironidae* and *Dorylaimida* has been postulated, with *Ironidae* representing the ancestral type.

COMPARISON OF THE MAIN FEATURES OF IRONIDAE AND DORYLAIMIDA

Differences can be observed in e.g. the number and position of the lips (except *Ironella*), structure and outlet of the excretory system, position of the oesophageal gland outlets and habitat of most representatives.

Similarities exist in general body shape, position and shape of the amphideal fovea, structure of the feeding apparatus, structure of the female reproductive system and of the male copulatory apparatus. It is clear that the *Dorylaimida*, having ordinal rank, are more heterogenous than the *Ironidae*, even though they may represent a superfamily. Therefore it is necessary to mention briefly the main characters of the subdivisions that have to be compared (Classification according to Coomans and Loof, 1970).

Suborder *Mononchina* : oesophagostome (1) (commonly called stoma or buccal cavity) barrel-shaped with heavily sclerotized walls, with 1-3 large teeth. If only one large tooth is present it is the dorsal one. Anterior somatic muscles controlling

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(1) Modification of the term oesophastome used by Inglis (1966) and Coomans (1975).

protrusion and retraction of oesophagostome, hence no real protractor muscles of the oesophagostome differentiated. Oesophagus cylindrical, with the dorsal gland nucleus (DN) far behind the outlet (DO) but anterior to the outlets of the first pair of ventrosublateral glands (S_1O). Excretory system usually obscure, but where observed consisting of two uninucleate long-necked renette cells connected to an ampulla and opening through an excretory pore situated behind the nerve ring. Caudal glands present or absent.

Suborder *Bathyodontina* : oesophagostome consisting of a wider anterior and narrower posterior portion, with weakly to strongly sclerotized walls and only one tooth of varying size but ventrosublateral in position. Protractor muscles of the oesophagostome differentiated, posteriorly attached to the oesophageal wall. Oesophagus cylindrical, with DN far behind DO, at the level of or behind S_1O. Excretory system obscure, pore situated behind nerve ring. Caudal glands present. This suborder comprises two superfamilies which show some important differences : (1) *Bathyodontoidea* have a narrow elongated oesophagostome, with a very small tooth and weakly sclerotized walls ; the second pair of ventrosublateral nuclei S_2N lies far behind the outlets (S_2O) ; cardiac glands lacking. (2) *Mononchuloidea* have a wide anterior oesophagostome with a large, grooved tooth and well sclerotized walls, S_2N lie opposite S_2O ; cardiac glands present.

Suborder *Dorylaimina* : oesophagostome with a long and narrow tooth or odontostyle of ventrosublateral origin, and weakly sclerotized walls. Well developed protractor muscles posteriorly attached to the oesophageal wall. Oesophagus consisting of a narrow anterior part and a wider posterior one. DN a short distance behind DO, well anterior to S_1O ; S_1N opposite S_1O. Excretory system and pore obscure. Caudal glands absent. Although several superfamilies have been proposed, only two are accepted : (1) *Nygolaimoidea* with ventrosublateral tooth and free cardiac glands ; both S_1N at about the same level and equally developed. (2) *Dorylaimoidea* with an axial odontostyle and usually no free cardiac glands ; S_1N usually at different levels and S_1N_1 often smaller than S_1N_2.

Two more suborders (*Diphtherophorina* and *Trichosyringina*) show a number of specialised and aberrant characters that obscure their origin. This is especially so for the *Diphtherophorina*. The *Trichosyringina* can be related to the *Dorylaimina* on the basis of their juvenile stages. Both groups however are not essential for the discussion below since they are by no means primitive dorylaims.

Family *Enoplidae* : oesophagostome consisting of two parts : (1) a double walled anterior part with three single, two single ventrosublateral and one double dorsal or a single dorsal and two double ventrosublateral teeth ; (2) an elongated odontophore region. Protractor muscles controlling protrusion of oesophagostome intra-oesophageal ; 4 retractor muscles outside oesophagus. Oesophagus cylindrical with 5 glands, the nuclei of which occur at the basis of the oesophagus ; outlets only known for the anterior three glands : S_1O anterior to DO. Excretory system consisting of a well developed, single renette cell, opening medio-ventrally between the first and second circlet of cephalic sense organs. Caudal glands usually present.

The family can be subdivided into two subfamilies : (1) *Ironinae* with anteriorly attenuating body ; relatively narrow mouth opening ; usually flattened spicules, usually with median sclerotization and ventral flange ; gubernaculum with sclerotized proximal and lateral margins of the corpus ; and (2) *Coniliinae* n. subf. : Ironidae. Body cylindrical. Mouth opening wide ; cheilostome forming a wide cylinder. Spicules long and tubiform. Type genus : *Conilia* GERLACH, 1956 ; other genus : *Ironella* COBB, 1920.

In Ironidae as well as *Dorylaimida* the anterior part of the feeding apparatus (modified anterior feeding apparatus or oesophagostome) shows a marked tendency to become elongated. In *Ironidae* typically three teeth are present, although the dorsal one is often and both ventrosublateral ones are rarely (*Ironella*) double. Within the *Dorylaimida* three teeth only occur in the *Mononchina*, while the other forms possess one tooth ; even in *Mononchina* there is a tendency towards a reduction of the two ventrosublateral teeth.

So we see that the occurrence of three teeth in the *Dorylaimida* is rather exceptional and, if so, the oesophagostome is not elongated. In those cases where the oesophagostome is elongated its lining provides a long supporting structure (odontophore) and is partly double walled enabling a forward movement of the whole system, so that teeth or tooth can protrude from the mouth for seizing or puncturing the prey. In *Ironidae* protraction of the oesophagostome is mediated by three protractors confined within the oesophageal wall (one per sector), while the inclination of the teeth is operated by separate muscles also inside the oesophageal wall (cf. VAN DER HEIDEN, 1975). In *Dorylaimida* this protraction typically is controlled by eight protractor muscles lying outside the oesophageal wall, but usually posteriorly attached to it. The retraction system is similar in both groups in that the retractor muscles are outside the oesophageal wall, attach to it anteriorly and to the body wall posteriorly. However, the number and position of retractor muscles are different : typically four (two subventral and two laterodorsal) in *Ironidae*, typically eight submedian ones in *Dorylaimida*.

In both groups the teeth (or tooth) are (is) replaced during moulting by replacement teeth (tooth) formed during the previous moulting and stored behind the functional teeth (tooth). *Ironidae* - juveniles have their replacement teeth about one lip-region width (or even more) behind the functional ones. That is compared to teeth-size rather far behind, compared to oesophagostomal length rather anterior. In *Mononchina* the replacement teeth are stored partly inside the functional ones ; in *Bathyodontina* the replacement tooth occurs immediately behind the functional one ; in *Nygolaimoidea* the replacement tooth is formed a short distance behind the functional one, whereas in *Dorylaimoidea* this situation only occurs in the first stage juveniles. Indeed, in the other juvenile stages the replacement odontostyle — although formed at the same place as in first stage juveniles, i.e. within the region of the odontophore — is shifted far posteriad.

The oesophagus of *Enoplidae* as well as this of the most primitive *Dorylaimida* is cylindrical ; in both groups its lining is provided with cuticular thickenings for muscle attachment. In *Dorylaimida* none of the oesophageal gland outlets lies anterior to the nerve ring and the dorsal gland outlet is the most anterior one ; the nuclei are normally not concentrated at the base of the oesophagus. In *Ironidae* three oesophageal glands open into the oesophagostome and the opening of the dorsal gland is preceeded by those of the ventrosublateral ones ; the nuclei are concentrated at the base of the oesophagus.

The excretory system of *Ironidae* consists of a longnecked single cell leading to a medioventral pore situated between the first and second circlet of cephalic sense organs ; the cell body occurs near the base of the oesophagus. In *Dorylaimida* the excretory system seems to be degenerate or at least obscure. In those forms for which the system has been reported (some *Mononchida*, *Longidorus*) it consists of two cells whose ducts join before opening through a pore that usually is situated just behind the nerve ring. The structure of the reproductive systems is variable from rather simple to very complicated especially in *Ironidae*, but leaving apart the secondary complications, the male as well as the female reproductive system of both groups resemble each other in gross morphology. The greatest variation is found in the uterus and although this may be useful to differentiate between the lower taxa, it is not reliable to trace evolutionary lines between higher ones. Until more is known about the cellular anatomy of the systems in both groups comparisons are difficult.

DISCUSSION

A critical appraisal of the similarities between *Ironidae* and *Dorylaimida* leads to the conclusion that they more likely are the result of parallel evolution rather than of close relationship.

The mechanism by which teeth, tooth-like structures or spears are protruded by the action of protractor muscles upon a rigid, sclerotized tube has originated independently in several groups of nematodes. The elongation of the anterior feeding apparatus is apparently advantageous for the functioning of such a system. An elongation has been achieved in all *Ironidae* and concerns the odontophore region, but has only been fully achieved in the more specialised *Dorylaimida* where it also concerns the tooth and the region around it. The elongation apparently was not present in the ancestral form of the *Dorylaimida* and originated within the group, probably in two steps ; it was accompanied by a reduction of the teeth to one. The protractor system in *Ironidae* is clearly of oesophageal origin, that of *Dorylaimida* may be of somatic origin or derived from the sheath that surround the oesophagus. Tooth formation and especially storage of a replacement tooth at some distance behind a functional one is correlated with tooth-size, thickness of the oesophagostomal wall and with the functioning of the anterior feeding apparatus. The phenomenon occurs also in other groups (cf. *Chromadorida*), though less pronounced. In any case it is evident that the condition in which the replacement tooth is stored at some distance behind the functional one has been achieved independently in *Ironidae* and *Dorylaimida*. Indeed, the most primitive *Dorylaimida* have the replacement tooth inside or immediately behind the functional one.

Cuticular thickenings of the oesophageal lining for muscle attachment are rather rare outside *Ironidae* and *Dorylaimida*, they are nevertheless occasionally found in other forms (e.g. *Eurystomina* and *Thoracostoma*, cf. CHITWOOD & CHITWOOD, 1950).

An important difference seems the position of the nuclei and outlets of the oesophageal glands. Since all *Dorylaimida* are comparable in having the outlets and nuclei behind the nerve ring this character was probably present in the ancestral form. On the other hand it should be stressed that this difference may not be overemphasized. Indeed, no other group has developed this situation and hence it can be considered as something typical for *Dorylaimida* (a synapomorphy). Little information is available about the excretory system of *Dorylaimida* except that it usually is considered to be reduced. If the systems so far described represent the typical situation, it is basically different from that of *Ironidae*.

So, while a number of differences can be attributed to special adaptions within each group, some of them seem to be fundamental. In the past the *Ironidae* too often have been compared with the more specialised *Dorylaimina*, while the more primitive *Mononchina* and *Bathyodontina* were overlooked. Therefore it seems that at present sufficient knowledge is lacking to say that the *Dorylaimida* originated from forms near the *Ironidae*.

Fig. 1

Possible evolution of Ironidae and Dorylaimida from Enoplida ancestor.

P = plesiomorph A = apomorph

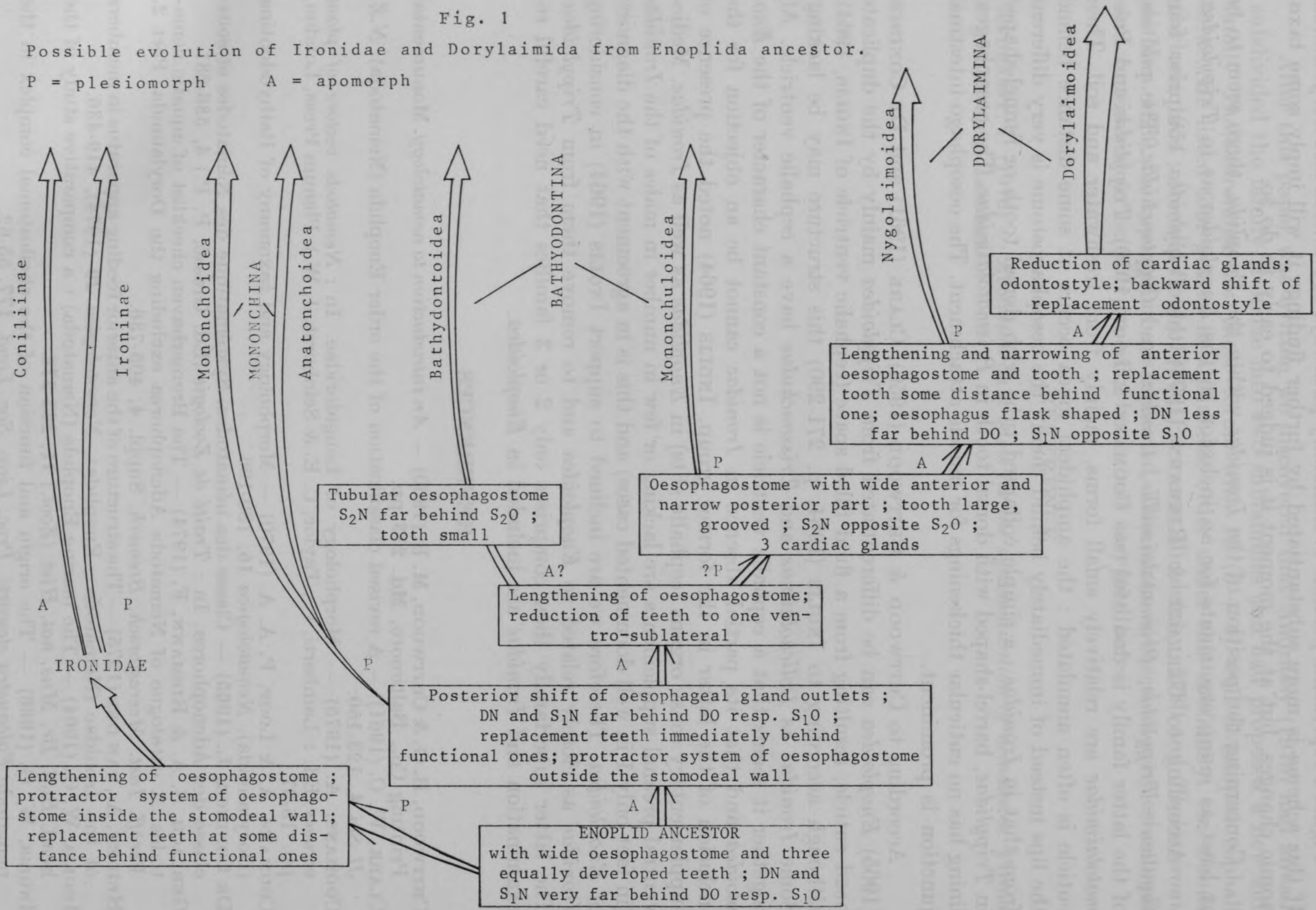

Figure 1 represents possible evolutionary pathways of *Ironidae* and *Dorylaimida*. If this scheme is more substantiated by further findings it will imply some taxonomic changes, but at the moment it is judged to early to do so.

Concerning the position of the *Ironidae* within the *Enoplida*, there seem to be at least as many arguments for an inclusion in the *Enoploidea* as in *Tripyloidea*.

According to GERLACH & RIEMANN (1974) the *Tripyloidea* comprise four families : *Tripylidae*, *Prismatolaimidae*, *Ironidae* and *Cryptonchidae*. The position of the latter family is doubtful (see COOMANS & LOOF, 1970). *Tripylidae* and *Prismatolaimidae* are relatively small forms, mainly from freshwater and soil. Their cuticle is often annulated ; the amphideal fovea occurs at some distance behind the lips instead of immediately behind them ; the oesophagostome is very different from that in *Ironidae* : a simple collapsed tube with dorsal tooth or funnel-shaped in *Tripylidae*, barrel-shaped with dorsal tooth in *Prismatolaimidae*. The oesophageal lining has no cuticular thickenings for muscle attachment. The oesophago-intestinal junction is prominent.

According to CHITWOOD & CHITWOOD (1950), CLARK (1961) and DE CONINCK (1965) *Enoploidea* can be differentiated from *Tripyloidea* mainly by the duplicate head cuticle, resulting from a fluid filled space (cephalic ventricle of INGLIS, 1964), although according to INGLIS (1964, p. 271-290) this structure may be lacking. Some *Ironidae* as *Dolicholaimus* and *Trissonchulus* have a cephalic ventricle. All together it seems that a cephalic ventricle is not a constant character of the *Enoploidea* and that its partial absence in *Ironidae* cannot be an objection for the inclusion of the latter in the former group. INGLIS (1964) noted the presence of supplementary sense organs (cephalic slits) in *Enoplidae* as well as *Ironidae*. Medioventral preanal supplements are lacking or few in number in males of the *Ironidae* (in fact only 1 in well documented cases) and this is in agreement with the diagnosis of *Enoploidea*. Therefore we are inclined to support INGLIS (1964) in considering *Ironidae* as closely related to *Enoploidea* and to remove them from *Tripyloidea*. The latter superfamily then comprises only 2 or 3 families that need careful reexamination and *Ironidae* are included in *Enoploidea*.

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ADDENDUM

After this paper was written we discovered that Andrássy (1976) had already subdivided the family Ironidae into two subfamilies and had proposed a new subfamily Thalassironinae for those forms with 10 (6 + 4) well developed cephalic setae. He listed four genera in alphabetic order under this subfamily, viz. *Conilia* Gerlach, 1954 ; *Ironella* Cobb, 1920 ; *Parironus* Micoletzky, 1930 and *Thalassironus* de Man, 1889. No type genus was indicated. This taxon is based on synplesiomorphy and considered to be polyphyletic, hence not accepted here.

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TAXONOMIC PROBLEMS WITHIN THE DESMOSCOLECIDA (NEMATODA)

by

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ABSTRACT

A few examples are given of variability and taxonomic difficulties within the Desmoscolecida as well at species level as at genus level. The diagnostic characters generally used within two genera : *Desmoscolex* CLAPARÈDE, 1863 and *Tricoma* COBB, 1894 and the status of the genus *Quadricoma* FILIPJEV, 1922 are discussed.

INTRODUCTION

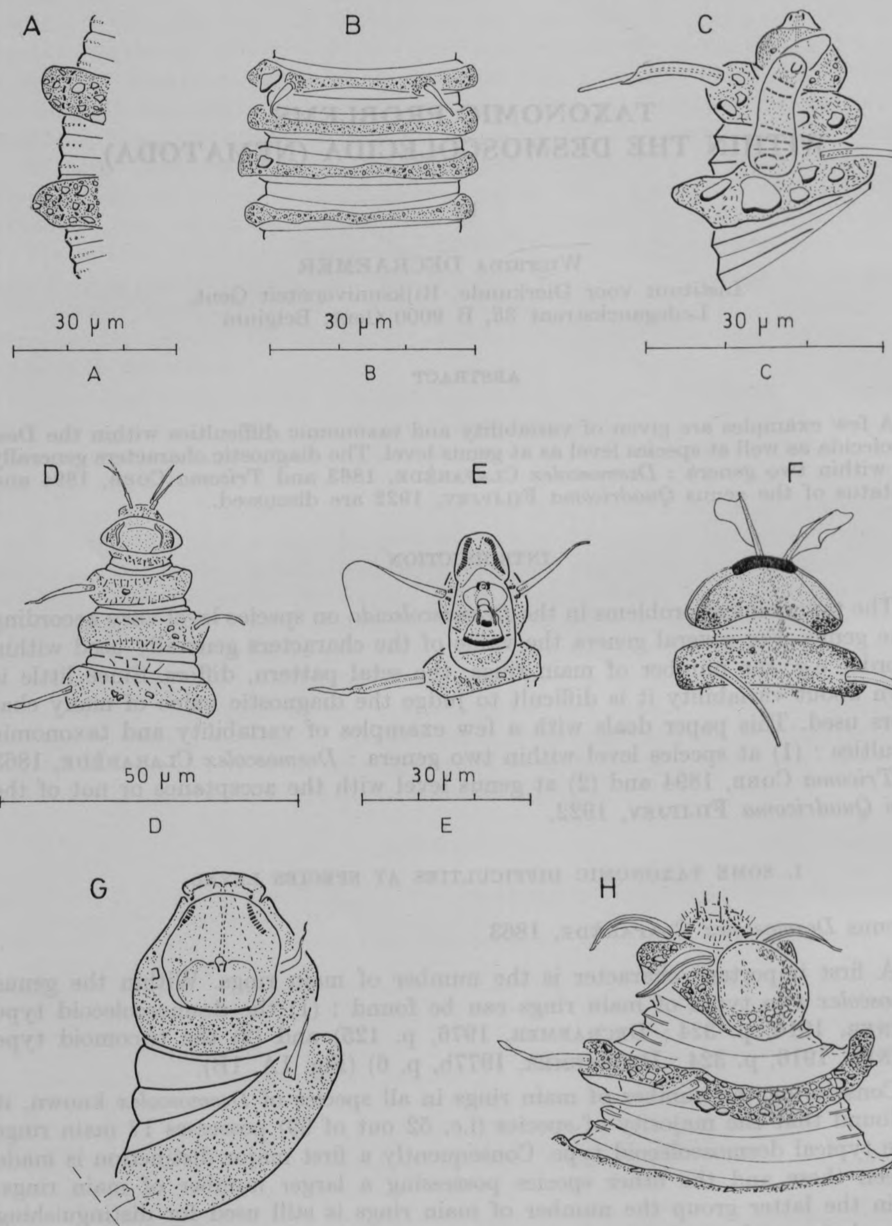
The taxonomical problems in the *Desmoscolecida* on species level vary according to the genus. For several genera the value of the characters generally used within the order e.g. the number of main rings, the setal pattern, differs. Since little is known about variability it is difficult to judge the diagnostic value of many characters used. This paper deals with a few examples of variability and taxonomic difficulties : (1) at species level within two genera : *Desmoscolex* CLARARÈDE, 1863 and *Tricoma* COBB, 1894 and (2) at genus level with the acceptance or not of the genus *Quadricoma* FILIPJEV, 1922.

I. SOME TAXONOMIC DIFFICULTIES AT SPECIES LEVEL

1. Genus *Desmoscolex* CLAPARÈDE, 1863

A first important character is the number of main rings. Within the genus *Desmoscolex* two types of main rings can be found : (1) the desmoscolecoid type (STEINER, 1916, p. 324 ; DECRAEMER, 1976, p. 125) and (2) the tricomoid type (STEINER, 1916, p. 324 ; DECRAEMER, 1977b, p. 6) (Fig. 1A, 1B).

Considering the number of main rings in all species of *Desmoscolex* known, it was found that the majority of species (i.e. 52 out of 69) possesses 17 main rings of the typical desmoscolecoid type. Consequently a first major distinction is made between these and the other species possessing a larger number of main rings. Within the latter group the number of main rings is still used for distinguishing further between 8 species having 18 main rings of desmoscolecoid type (in two species one animal formed an exception with 19 rings) and the remaining species with 22-44 main rings. Among the latter group the species with the largest number of main rings, i.e. from about 29 rings on have a tricomoid type of main ring ; thus in the group containing the species with the largest number of rings the type of main ring is used as an additional diagnostic character.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Only two examples of sexual dimorphism in the number of main rings are known : *D. aquaedulcis* STAMMER, 1935 with 18 rings in males, 22 rings in females and *D. velifer* TIMM, 1970 with 43-44 rings in males, 31-38 rings in females.

Some variability in the number of main rings occurs in the species with a number of rings higher than 25 (e.g. in *D. vinealis* WEISCHER, 1962 : 11♀♀ with 25-29 rings). Among the 17-ring species no variability in the number of rings was ever noticed except for *D. geraerti* DECRAEMER, 1974 were a male specimen was found with only 16 rings ; it was however considered as aberrant and having lost a ring between its 8th and 9th main ring as could be deduced from the setal pattern.

A second important diagnostic character in *Desmoscolex* is the setal pattern. Departures from the typical scheme for 17-ring species (TIMM, 1970) are characteristic for a given species. In a few species e.g. *D. dimorphus* DECRAEMER, 1975, *D. sieverti* FREUDENHAMMER, 1975 sexual dimorphism occurs in the setal pattern. As far as I know, apart from sexual dimorphism, only one example *D. falcatus* LORENZEN, 1969 was found showing an intraspecific variability in the setal pattern among specimens from different localities (cf. DECRAEMER, 1975, p. 248).

Third, the head shape, the shape and length of the amphids (cf. Fig. 1C-1G) are usually of taxonomic value e.g. the possession of a rostrum (Fig. 1C) and the elongation of the amphids as in *D. asetosus* DECRAEMER, 1975. However several species may posses a similar head structure as e.g. in *D. geraerti*, *D. nymphianus* DECRAEMER, 1974, *D. brevisetosus* DECRAEMER, 1974.

Fourth, the presence or absence of cephalic setae, their length, shape (with or without a membrane) and the position of the cephalic setae on the head are of great diagnostic value (Fig. 1C-1H).

In males the copulatory apparatus, mainly the length and shape of the spicules may be of diagnostic value ; the gubernaculum can rarely be used since it often is lacking or if present it consists of a thin trough-like structure parallel to the spicules in about all the species known so far.

Additional characters such as the shape and length of the end rings and spinneret, the structure of the cuticular rings (with or without spines or pores) are often given some diagnostic value.

Fig. 1. — Genus *Desmoscolex*

A : *D. asetosus* (♂) : detail of dorsal body wall at the level of main rings 10 and 11 : desmoscolecoid type (cf DECRAEMER, 1976)

B : *D. labiosus* (♀ : nr. 4454 Landbouwhogeschool, Wageningen) : surface view of part of body wall at the level of main rings 9-12 : tricomoid type (cf DECRAEMER, 1976)

C : *D. asetosus* : surface view of head, lateral side (♂) (cf DECRAEMER, 1975)

D : *D. leptus* : surface view of head, lateral side (♀) (cf DECRAEMER, 1975)

E : *D. longisetosus* : surface view of head, lateral side (holotype ♂) (cf DECRAEMER, 1975)

F : *D. spinosus* : surface view of head, lateral side (♀) (cf DECRAEMER, 1976)

G : *D. falcatus* : surface view of head, lateral side (holotype ♂) (cf DECRAEMER, 1974)

H : *D. velifer* : surface view of head, dorsal side (♂) (cf TIMM, 1970, fig. 41).

Conclusion

Considering the diagnostic value of the number of main rings we can conclude that when that number is low, it is constant and when it is higher, then its diagnostic value is more limited and a certain range of variability should be taken into account. As appears from the data mentioned above, most characters used to characterize species and to distinguish them from one another are surface ones, which give only a partial picture of the structure and may be more subjected to variation than internal features. Detailed morphological studies of the anatomy of many species of *Desmoscolex* (DECRAEMER, 1976) showed a large similarity between them. Consequently at the present time the internal organs can rarely be of any use for distinguishing species. In future further detailed studies of the female reproductive system and of the anterior sensorial organs would presumably be of greater help in solving taxonomic problems within this group.

2. Genus *Tricoma* COBB, 1894

In this genus the taxonomic problems are even larger than in other genera of the *Desmoscolecida*. This is due to (1) the large number of species, (2) the many inaccurate and superficial descriptions and figures lacking data on internal organs, anterior sensorial structures and labial region, (3) descriptions based on a single specimen even when orientated in a dorso-ventral position, (4) the emphasis put on the number of main rings without taking into account the occurrence of a possible variation. Two species, *T. dimorpha* DECRAEMER, 1977 and *T. similis* COBB, 1912, illustrate the large variabilities that can occur in characters used as diagnostic features (such as the number of main rings, body length and genital setae). Both species are easily distinguished from all other species of the genus.

a) *Tricoma dimorpha* (Figs. 10, 11 in DECRAEMER, 1977b)

In a first study of the type material of *T. dimorpha* from Yonge Reef (Australia) a tentative distinction was made between two different forms based on a difference in the total number of main body rings and in the number of tail rings : (1) a « typical » form with 61-65 main rings and 12-13 tail rings in males ; 62-67 main rings and 12-13 tail rings in females and (2) an « aberrant » form with only male specimens having 52-54 main rings and 10-11 tail rings.

No differences were found between both forms in habitus, setal pattern, copulatory apparatus, internal organs and detailed morphology of the head region.

Later on, other specimens of *T. dimorpha* became available from Gannet Cay (Australia). Among them two male specimens were found possessing a number of main rings lying in between the range recorded for the « typical » and the « aberrant » form i.e. with 58 and 60 rings. The number of tail rings was respectively 11 and 12.

Taking into account the specimens from Gannet Cay, *T. dimorpha* can no longer be split up on the basis of the number of main rings since the larger the number of specimens available the greater the chance to cover completely the difference in number of main rings observed in the type material.

Apart from a variability in the number of main rings in *T. dimorpha* there was also a relative large variation in body length. One male and one female paratype were clearly longer than the other specimens : 600 μm (♂) against 305-370 μm (other males) ; 650 μm (♀) against 335-410 μm (other females).

b) *Tricoma similis* (cf. Figs. in Cobb, 1912 ; Figs. 30-35 in Decraemer, 1977b)

In *T. similis* the following variations were found in diagnostic features : (1) the number of main rings varies between 80 and 85 in males and between 77 and 84 in females, (2) in males the number and position of the genital setae (mostly 2 setae situated on rings 55 and 57) varies between 1 and 3 setae situated between rings 52 and 62 and (3) in females the position of the vulva varies from ring 43-46 or interzones 43-44, 44-45.

Apart from the number of main rings, following characters are used as diagnostic features : the setal pattern, the head- and amphid-shape, the length and shape of spicules and gubernaculum. More recently (Decraemer, 1977b) an attempt was made to study the internal organs, the labial region and anterior sensorial organs more in detail so that they could also be used in solving taxonomic problems.

Considering the setal pattern, it was found that the number of subdorsal setae is mostly constant within the same species and differs only slightly among species with 9, 11 and 13 pairs as most frequent numbers. The subventral setae vary in number within the species and among different species.

Conclusion

From the large intraspecific variation observed in the number of main rings in *T. dimorpha* we can conclude that this character generally accepted as the most or one of the most important diagnostic features in the genus *Tricoma*, is of more limited value. The number of main rings may be helpful for the identification of species, but should not be overweighted especially since for the majority of the species nothing is known about its variability.

The diagnostic value of the setal pattern in the genus *Tricoma* is more limited compared with that in *Desmoscolex* (see above).

II. TAXONOMIC DIFFICULTIES AT THE GENUS LEVEL

Some taxonomic problems of the *Desmoscolecida* exist at the generic level e.g. the status of the genus *Quadricoma* Filipjev, 1922.

The original diagnosis of Filipjev (1922) is of little use, but on the basis of characters of the type species *Quadricoma loricata* Filipjev, 1922 (cf. also Decraemer, 1978) the genus can be clearly distinguished from other genera.

In contradiction with Lorenzen (1969) who synonymized without comment *Quadricoma* with *Tricoma* while introducing a new subfamily Tricominae, I am inclined to follow Timm (1970) and Freudenhammer (1975) who considered *Quadricoma* as a separate genus.

However, the differences between both genera : *Quadricoma* and *Tricoma* are relatively small. The main difference is found in the shape of the main rings i.e. all main rings quadricomoid and with a clear ring of inversion in *Quadricoma* (see Timm, 1970, p. 38 ; Decraemer, 1978) while in *Tricoma* the main rings are mainly tricomoid except for those in the extreme anterior body region and tail which may be quadricomoid in some species ; an inversion rings is always lacking (Fig. 2A, 2B, 2D).

Among the type material of *Q. noffsingerae* Decraemer, 1977 a male and a female specimen were found possessing (as opposed to the other specimens) only quadricomoid rings in the anterior part of the body and in the tail region ; the rings

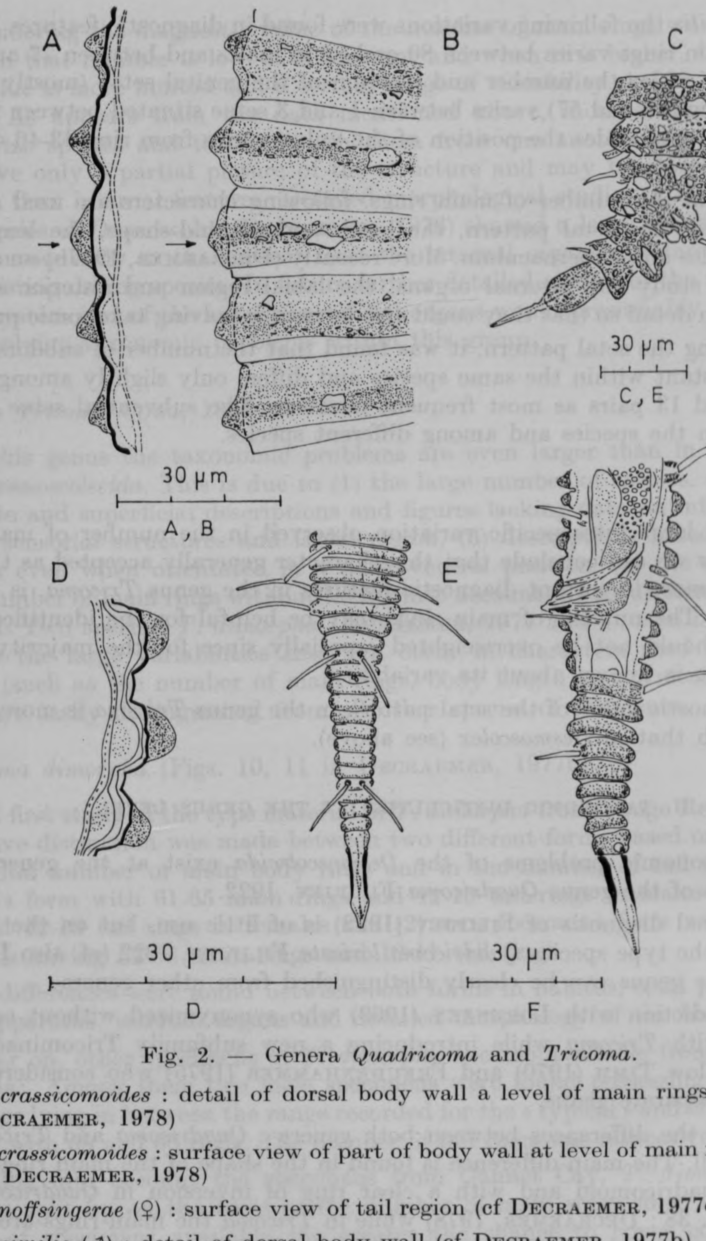

Fig. 2. — Genera *Quadricoma* and *Tricoma*.

A : *Q. crassicomoides* : detail of dorsal body wall a level of main rings 29 and 33 (cf DECRAEMER, 1978)

B : *Q. crassicomoides* : surface view of part of body wall at level of main rings 29 and 33 (cf DECRAEMER, 1978)

C : *Q. noffsingerae* (♀) : surface view of tail region (cf DECRAEMER, 1977c)

D : *T. similis* (♂) : detail of dorsal body wall (cf DECRAEMER, 1977b)

E : *T. dimorpha* : surface view of the ventral side of the posterior body region of a female (cf DECRAEMER, 1977b)

F : *T. dimorpha* : posterior body region of a male (cf DECRAEMER, 1977b).

situated in between are tricomoid, also due to the absence of foreign material on the interzones. Consequently no ring of inversion was observed in both specimens. If only a specimen was found showing the aberrance in the structure of the main rings the definition of the genus based only on the shape on the rings would be uncertain.

However, apart from the structure of the main rings additional characters may be used in distinguishing both genera i.e. (1) the shape of the endring and spinneret. In *Quadricoma* the spinneret consists of a fine, elongated, naked structure, offset from the broader covered anterior part of the end ring ; in *Tricoma* the naked spinneret is short, not offset from the covered anterior part of the end ring which gradually tapers posteriorly. (2) The shape of the head : the conspicuous triangular head shape in lateral view typical for *Tricoma*, is not present in *Quadricoma*.

Conclusion

Since the genus *Quadricoma* can be clearly distinguished from *Tricoma* mainly on the base of the structure of the main rings and since until now as far as I know only one exception (*Q. noffsingerae*) exists I tentatively recognize *Quadricoma* as a separate genus for practical reasons and until more detailed studies of both genera will allow well founded conclusions.

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THE SYSTEM OF THE MONHYSTEROIDEA (NEMATODES) A NEW APPROACH

by

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SUMMARY

In 131 marine, brackish, limnic and terrestrial species of the superfamily Monhysteroidea the following characters have been studied and evaluated phylogenetically : structure of the cuticle ; presence of ocelli ; structure of the amphids ; number, structure and length ratio of the cephalic setae ; presence and postembryonic development of subcephalic setae ; structure of the buccal cavity ; presence and position of the excretory gland and its opening ; number of testes ; position of the testes and the ovary relative to the intestine ; structure of the tail. As a result of this study an argumentation scheme is presented to demonstrate the phylogenetic relationship between the three families of the Monhysteroidea. These are :

1. Monhysteridae de Man 1876
2. Xyalidae Chitwood 1951
   Cobbiinae de Coninck 1965, syn. n.
   Rhynchonematinae de Coninck 1965, syn. n.
   Scaptrellidae de Coninck 1965, syn. n.
3. Sphaerolaimidae Filipjev 1918, with two subfamilies :
   Sphaerolaiminae Filipjev 1918
   Parasphaerolaiminae Lorenzen 1978

The greatest taxonomic change is the splitting up of the Monhysteridae into Monhysteridae *sensu stricto* and Xyalidae. Both families are mainly distinguished on the basis of the cuticle (smooth in Monhysteridae, annulated in Xyalidae), the number of testes (always one in Monhysteridae, mostly two in Xyalidae), and the position of the gonads relative to the intestine (anterior testis and ovary on the right side in Monhysteridae and on the left side in Xyalidae ; posterior testis lacking in Monhysteridae and on the right side in Xyalidae). The distinction is matched by different ecological distribution, the Monhysteridae being predominantly brackish, limnic and terrestrial, the Xyalidae predominantly marine and brackish. It is assumed that the Monhysteridae live primarily in brackish and limnic biotopes and only secondarily in marine ones.

The Sphaerolaimidae live in marine and brackish biotopes. They differ mainly

from both the Monhysteridae and the Xyalidae in that the position of the gonads is variable. The Sphaerolaimidae are more closely related to the Xyalidae than to the Monhysteridae.

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A REVISION OF THE MICROLAIMIDAE, DESCRIPTION OF THE MOLGOLAIMIDAE N. FAM. AND REMARKS ON THE SYSTEMATIC POSITION OF *PARAMICROLAIMUS* (FREE-LIVING NEMATODES)

by

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SUMMARY

The up to now classified species of Microlaimidae (Nematoda, Desmodorida) are herein revised and a diagnosis, discussion and keys to each of the groups treated are given with the exception of keys to the species of *Microlaimus* and *Prodesmodora*.

The main differentiating characters applied are : the structure of the head region (cephalic sense organs, amphids and buccal cavity), shape of the oesophagus, position of the excretory pore, shape of the tail, the gonads and the cuticle. The presence of porids and preanal supplements is stressed and their significance as distinguishing characters is discussed.

The family Microlaimidae contains Bolbolaiminae n. subfam. (*Bolbolaimus* syn. *Pseudomicrolaimus*) and Microlaiminae (*Calomicrolaimus*, *Ixonema* and *Microlaimus*), distinguished by the situation of the cephalic sense organs, sclerotization of the buccal cavity, shape of the oesophagus and structure of the copulatory apparatus. Microlaimidae is closely related to Desmodoridae.

Molgolaimidae n. fam. is established in order to accomodate species with a weakly developed head region, oval to spherical bulb of oesophagus, excretory pore anterior to nerve ring, posterior portion of tail cylindrical, ovaries usually reflexed and smooth or striate cuticle, i.e., Aponematinae n. subfam. (*Aponema* n. gen.) and Molgolaiminae n. subfam. (*Molgolaimus* and *Prodesmodora*), distinguished by the sclerotization of the amphids and structure of the copulatory apparatus. Molgolaimidae n. fam. is closely related to Spiriniidae.

Paramicrolaimus is removed from the Microlaimidae and transferred to the Spiriniidae ; it is closely related to the genera of Stilbonematinae.

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A REVIEW OF THE COMESOMATIDAE (FREE-LIVING MARINE NEMATODES)

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SUMMARY

The Comesomatidae are among the most abundant nematodes in soft bottom sediments, and meiofaunal studies have shown that in a given locality 1-3 species may represent more than 40 % of the total nematode population (Table 1).

Based on studies of a large material from the Øresund (Denmark) and museum material with ligth microscopy, the gross and fine morphology of the family is reviewed and the systematic position of its members revised. A diagnosis, discussion and keys to each of the groups treated are given. For classification the following three main characters are used : the buccal cavity, the structure of the copulatory apparatus and the arrangement of the cephalic sense organs. A copulatory apparatus provided with apophyses and a female reproductive system with outstretched ovaries are considered as significant characters of the Comesomatidae within the Chromadorida. The presence of marginal tubes within the oesophagus, and a non-sclerotized and enlarged symmetrical tail tip are further distinguishing characters.

The structure of the *Sabatieria* type (Sabatieriinae) is considered basic ; from this condition the *Cervonema* type is derived with reduced characters, while representatives of Dorylaimopsinae and Comesomatinae show highly specialized conditions.

The genera are rearranged in three subfamilies as follows :

Sabatieriinae : *Cervonema*, *Laimella*, *Pierrickia*, *Sabatieria* (syn. *Actarjania*), *Scholpaniella*.

Dorylaimopsinae : *Dorylaimopsis* (syn. *Mesonchium*), *Hopperia*, *Metasabatieria*, *Paramesonchium*, *Vasostoma*.

Comesomatinae : *Comesoma*, *Metacomesoma*, *Paracomesoma*.

Acantholaiminae has been removed from the Comesomatidae because they show a closer relationship to the Neotonchinae (Cyatholaimidae).

TABLE 1

Mean dominance values of Comesomatidae in marine sediments

Study data	Mean Dominance of Comesomatidae : Total nematode fauna	Abundant Comesomatidae species
Øresund		
Present study		
Hornbæk		
silty sand, *Haploops* community, 28 m		
Station I (few *Haploops*)	42 %	*Dorylaimopsis punctata*, *Sabatieria ornata*, *S.* aff. *pulchra*,
Station II (many *Haploops*)	42 %	*D. punctata*, *S. ornata*
North Sea		
Mc Intyre (1961)		Comesomatidae and Oncholaimidae more than 50 % dominance ; *D. punctata*, *S. celtica* (1)
Fladen Grund		
silt, 146 m	?	
Loch Nevis		
silty clay, 90-100 m	?	
Warwick & Buchanan (1970)		
Northumberland		
St. A fine sand, 35 m	27 %	*S. ornata*, *D. punctaia*
St. B fine sand, 54 m	24 %	*S. ornata*
St. C silty sand, 80 m	38 %	*D. punctata*, *S. celtica* (1), *S. ornata*
Warwick & Buchanan (1971)		
Northumberland		
St. C silty sand, 80 m	18-37 %	*D. punctata*, *S. celtica* (1) *S. ornata*
Ward (1973)		
Liverpool Bay		
Habitat 1-6, silty sand	14 % (2-70 %)	*Sabatieria* sp.
Lorenzen (1974)		
German Bight		
Titan disposal, fine sand, 23-27 m	17 %	*S. celtica*
St. A of Rachor, silt, 20-25 m	58 %	*S. pulchra*
St. B of Rachor, silty sand, 35 m	36 %	*S. pulchra*
Juario (1975)		
German Bight		
St. Alt P 12, silty sand, 35 m	18 %	*S. pulchra*

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(1) As *Sabatieria cupida*.

Study data	Mean Dominance of Comesomatidae : Total nematode fauna	Abundant Comesomatidae species
Mediterranean		
BOUCHER (1973)		
Banyuls-sur-Mer		
silt, 35 m	54 %	*S. proabyssalis*, *D. mediterranea*, *S. granulosa*
VITIELLO (1974)		
Marseilles		*S. proabyssalis*, *S. pulchra* (2), *S. granulosa* *D. mediterranea*
St. 41-50, silt, 2-6 m	10 %	
St. 51-60, silt, 49-80 m	64 %	
VITIELLO (1976)		
Marseilles		
St. 61-70, silt, 55-82 m	35 %	*S. stekhoveni*
St. 71-80, silt, 310-650 m	39 %	
Black Sea		
GROZA-ROJANCOVSKY (1973)		*S. abyssalis*, dominant in all samples
mud, 19 samples	?	
Eastern North Atlantic		
WIESER (1960)		
Buzzards Bay		
St. P, fine sand, 18-30 m	16 %	*D. metatypicus*
TIETJEN (1971)		
Cape Lookout, silty sand, 600 m	17 %	*S. americana*
Cape Fear, silty sand, 800 m	14 %	*Comesoma* sp.
North Carolina, 750 m	41 %	*S. americana*
TIETJEN (1977)		
Long Island Sound		
St. 2, 7, 8, 13, 82, mud, 6-31 m	42 %	*S. pulchra*
St. 10, 86, 100, muddy sand, 5-28 m	23 %	*S. pulchra*
St. 25, 103, 105, 126, fine sand 5-21 m	20 %	*D. metatypicus*, *S. pulchra*
St. 14, 23, 67, 90, 128, 130, medium coarse sand	10 %	*S. hilarula*, *D. metatypicus*
GERLACH (1977)		
Bermuda		
medium calcareous sand, intertidal flat		
natural sand	24 %	*S. migrans*, *C. bermudense*
treated sand	48-72 %	

(2) As *Sabatieria vulgare*.

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FREE-LIVING MARINE NEMATODES (SUBCLASS ADENOPHOREA) OF THE RIA DESEADO (SANTA CRUZ, ARGENTINA)

Systematic contributions I

by

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ABSTRACT

The systematic study of twelve species of free-living marine nematodes of Puerto Deseado (Santa Cruz, Argentina) is dealt with. Seven of them, *Euchromadora permutabilis* WIESER ; *Steineridora archaica* (STEINER & HOEPPLI) ; *Paracanthonchus austrospectabilis* WIESER ; *Anoplostoma viviparum* WIESER ; *Anoplostoma camus* WIESER ; *Viscosia macramphida* CHITWOOD ; *Paramonohystera proteus* WIESER, are new records for our country. Morphological characteristics and original drawings are added.

INTRODUCTION

In Argentina, there are very few records about the subclass Adenophorea. There are incomplete descriptions of some species of free-living marine nematodes by ALLGÉN (1930-1959) in particular for the Fueguian Province (Falkland Island, States Island and Fueguian Archipelago), but for this province there are also excellent descriptions e.g. VON LINSTOW (1907) (Scottish National Antarctic Expedition), DE MAN (1904) (Belgian Antarctic Expedition) and COBB (1914 & 1930) (Shakleton Expedition and Australasian Antarctic Expedition).

Due to the important functions that these organisms have in the marine ecosystem, it is felt necessary to study them in our country.

In this work we only consider the nematodes living on seaweeds (true epiphytics and pseudoepiphytics).

Twelve species are described, seven of which are new records for our country. In addition, new data have been given for incompletely described species.

MATERIAL AND METHODS

The nematodes were recovered from 24 samples from « La Pesquera », locality situated in Ria Deseado, Puerto Deseado, Santa Cruz province, Argentina. Sixteen of these were taken in summer (23/1/1975) and eight in winter (6/6/1976), numbered 21-1 and 28 respectively.

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The locality is characterized by the fact that it has a sandstone bottom with an inclination of six degrees and a high deposit of slime. More detailed descriptions of this particular bottom have been given in previous works (ZAIXSO, 1975 ; ZAIXSO and PASTOR, 1976).

Samples were taken along a line runing from the lower supralittoral (LHS) to the transitional zone (TZ). Throughout this area, 200 grammes of different green, red and brown sea-weeds, typical of each horizon, were handpicked at lowtide.

In the lab the nematodes were picked out from amongst the sea-weeds with HOPPER's technique (HULINGS & GRAY, 1971) using a proportion of 4:1 sea-water to fresh-water.

They were fixed and dehydrated by DITLEVSEN's method (1911). They were mounted in glycerine-jelly. The drawings were made with a Wild drawing device. Spicules were measured along the curved median line. All samples are deposited in CIBIMA.

Abbreviations

LHS = Lower Horizon Supralittoral
UHM = Upper Horizon Mesolittoral
MHM = Middle Horizon Mesolittoral
LHM = Lower Horizon Mesolittoral
TZ = Transitional Zone = Infralittoral fringe
c.d. = Cephalic diameter
o.d. = Diameter at base of oesophagus
a.d. = Anal body diameter (in females)
cl.d. = Cloacal body diameter (in males)

SPECIES STUDIED

Euchromadora permutabilis
Steineridora archaica
Chromadora nudicapitata
Paracanthonchus austrospectabilis
Praeacanthonchus punctatus
Dolicholaimus marioni
Viscosia macramphida
Enoplus michaelseni
Anoplostoma viviparum
Anoplostoma camus
Paramonohystera proteus
Araeolaimus elegans

Euchromadora permutabilis WIESER, 1954
(Plate I, Fig. 1a-e)

Measurements : five males and five females, in µm.

Length of body : 2040 ; 2000 ; 2000 ; 1800 ; 1940 ; 2280 ; 2200 ; 2060 ; 2140 ; 2100

Length of oesophagus : 340 ; 310 ; 310 ; 310 ; 340 ; 360 ; 360 ; 310 ; 345 ; 380.

Maximum width : 100 ; 120 ; 100 ; 100 ; 100 ; 100 ; 160 ; 140 ; 140 ; 140.

Length of tail : 260 ; 200 ; 240 ; 210 ; 240 ; 200 ; 260 ; 160 ; 210 ; 210.

Length of spicules : 108 ; 108 ; 108 ; 100 ; 80 ; — ; — ; — ; — ; —.

Length of gubernaculum (lateral piece) : 55 ; 55 ; 55 ; 55 ; 45 ; — ; — ; — ; — ; —.
(dorsal piece) : 85 ; 87 ; 80 ; 85 ; 85 ; — ; — ; — ; — ; —.

V : — ; — ; — ; — ; — ; 52.5 ; 45.5 ; 44 ; 52.5 ; 53.5.

de Man's ratios : a = 20.4 ; 16.6 ; 20.0 ; 18.0 ; 19.4 ; 22.8 ; 13.7 ; 14.7 ; 15.3 ; 15.0 ; b = 6.0 ; 6.5 ; 6.5 ; 5.8 ; 5.7 ; 6.3 ; 6.1 ; 6.6 ; 6.2 ; 5.5 ; c = 7.8 ; 10.0 ; 8.3 ; 8.6 ; 8.1 ; 11.4 ; 11.0 ; 12.9 ; 10.2 ; 10.0

Description

Head : diameter 33 μm, with six external labial papillae and four cephalic setae (10 μm long). The amphids are slit-like and 2.3 c.d. The buccal cavity has twelve cheilorhabdia (5 μm long), that are followed by one big dorsal tooth (12 μm) with a small base and another subventral tooth (5 μm) that thins out at the end.

In males the spicules are slightly arched. The gubernaculum has a single dorsal piece and two lateral ones. The a.d. is 70 μm. The caudal glands are well developed.

Sample data : 21-1 : 4 (UHM) ; 5, 11, 15 (LHM) ; 28 : 1 (LHS), 5 (MHM), 11, 5 (LMH), 19 (TZ).

Geographic distribution : Chilean coast.

Remark

The specimens agree very well with the description given by WIESER (1954). This represents a new record for Argentina's coasts.

Steineridora archaica (STEINER & HOEPPLI, 1926) Inglis, 1969
(Plate I, Fig. 2a-g)

Measurements : four males and two females, in μm.

Length of body : 1800 ; 2100 ; 2200 ; 2000 ; 2200 ; 1900.

Length of oesophagus : 330 ; 330 ; 345 ; 315 ; 380 ; 340.

Maximum width : 100 ; 105 ; 105 ; 100 ; 125 ; 100.

Length of tail : 235 ; 210 ; 330 ; 220 ; 280 ; 220.

Length of spicules : 90 ; 95 ; 100 ; 90 ; — ; —.

Length of gubernaculum : 55 ; 55 ; 58 ; 60 ; — ; —.

V : — ; — ; — ; — ; 49 ; 50.5.

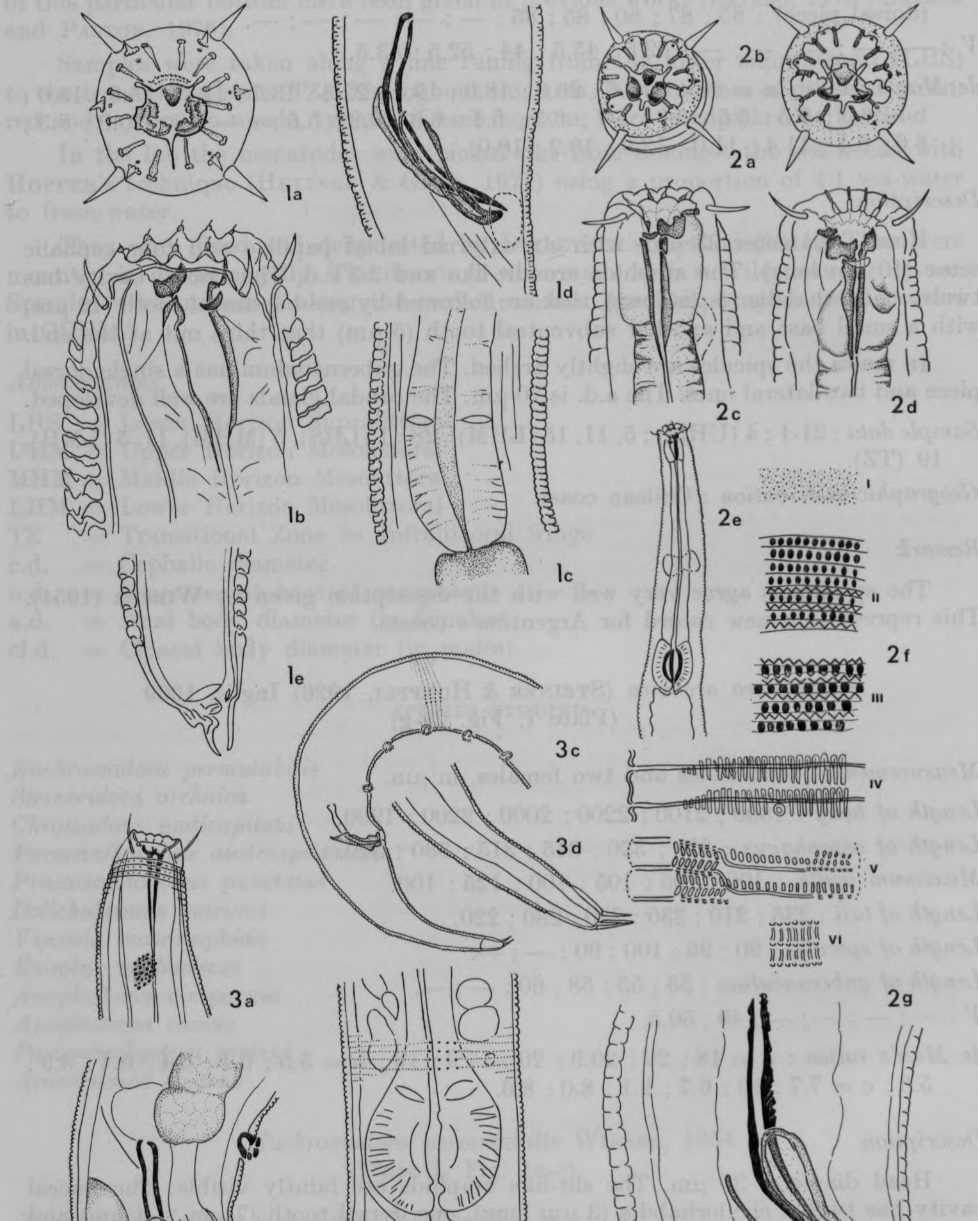
de Man's ratios : a = 18 ; 20 ; 20.9 ; 20 ; 17.9 ; 19 ; b = 5.5 ; 6.4 ; 6.4 ; 6.4 ; 5.9 ; 5.6 ; c = 7.7 ; 10 ; 6.7 ; 9.1 ; 8.0 ; 8.6.

Description

Head diameter 30 μm. The slit-like amphids are faintly visible. The buccal cavity has twelve cheilorhabdia (3 μm long), one dorsal tooth (7 μm × 4 μm) and two subventral teeth (6 μm). The ventrolateral walls of prostoma are sclerotized with a punctated surface.

The spicules are longer than in WIESER's specimens (75 μm). The same is true for the gubernaculum (lateral and dorsal piece according to Wieser 46 and 48 μm) but they maintain the same relation in a.d.

PLATE I


1a
1d
2b
2a
1b
1c
2c
2d
2e
i
ii
2f
iii
1e
3c
iv
3d
v
vi
3a
2g
3e
R
3b
A 40μm
B 40μm
C 100μm
D 20μm

Sample data : 21-1 : 3 (UHM), 3, 5 (MHM), 5 (LHM) ; 28 : 1 (LHS).

Geographic distribution : Japan, Chilean coast.

Remarks

The specimens agree very well with the description given by WIESER (1954). The species represents a new record for our country.

Chromadora nudicapitata BASTIAN, 1865

(Plate I, Fig. 3a-e)

Measurements : three males and three females, in μm.

Length of body : 743 ; 634 ; 857 ; 743 ; 914 ; 657.

Length of oesophagus : 120 ; 114 ; 114 ; 126 ; 171 ; 114.

Maximum width : 29 ; 30 ; 30 ; 103 ; 29 ; 30.

Length of tail : 86 ; 57 ; 69 ; 86 ; 114 ; 103.

Length of spicules : 26 ; 26 ; 29 ; — ; — ; —.

Length of gubernaculum : 17 ; 21 ; 17 ; — ; — ; —.

V : — ; — ; — ; 46 ; 47 ; 48.

de Man's ratios : a = 25.6 ; 21.1 ; 28.6 ; 21.7 ; 31.5 ; 21.9 ; b = 6.2 ; 5.6 ; 7.5 ; 5.9 ; 5.3 ; 5.8 ; c = 8.6 ; 11.1 ; 12.4 ; 8.6 ; 8.0 ; 6.4.

Sample data : 21-1 : 3, 4 (UHM), 3, 4, 5 (MHM), 10, 13, 15, 5, 11, 7 (LHM) ; 28 : 1 (LHS), 11, 5 (LHM).

Geographic distribution : cosmopolitan.

Remarks

The specimens agree very well with the original description given by BASTIAN (1865).

Paracanthonchus austrospectabilis WIESER, 1954

(Plate II, Fig. 4a-f)

Measurements : five males and three females, in μm.

Length of body : 1920 ; 1840 ; 1820 ; 1870 ; 1960 ; 1860 ; 1480 ; 1340.

Length of oesophagus : 320 ; 360 ; 400 ; 350 ; 380 ; 360 ; 360 ; 330.

PLATE I

Euchromadora permutabilis Fig. 1a-e : a) head, apical view ; b) head, lateral view ; c) oesophagus ; d) spicules ; e) tail.

Steineridora archaica Fig. 2a-g : a-b) head, apical view ; c-d) head, lateral view ; e) anterior end ; f) cuticle : I. on head at the top, II. on head over buccal cavity, III-IV. over oesophagus, V. on the middle of the body, VI. on tail ; g) spicules.

Chromadora nudicapitata Fig. 3a-e : a) head, apical view ; b) head, lateral view ; c) posterior end ; d) tail ; e) spicules.

Scales : A = 1c, d & 3c ; B = 2a-d, f & g ; C = 2e ; D = 1a, b & e, 3a, b, d & e.

Maximum width : 80 ; 70 ; 70 ; 80 ; 100 ; 100 ; 75 ; 110.

Length of tail : 140 ; 140 ; 110 ; 120 ; 110 ; 130 ; 120 ; 140.

Length of spicules : 72 ; 66 ; 66 ; 68 ; 68 ; — ; — ; —.

Length of gubernaculum : 58 ; 57 ; 58 ; 60 ; 62 ; — ; — ; —.

V : — ; — ; — ; — ; — ; 49.5 ; 52.5 ; 63.5.

de Man's ratios : a = 24.0 ; 20.4 ; 26.0 ; 23.4 ; 19.6 ; 18.6 ; 19.7 ; 18.2 ; b = 6.0 ; 5.1 ; 5.1 ; 4.7 ; 5.6 ; 4.9 ; 4.1 ; 4.1 ; c = 13.7 ; 13.1 ; 16.2 ; 15.6 ; 17.8 ; 14.3 ; 12.3 ; 9.6.

Description

The buccal cavity is formed by twelve cheilorhabdia 7 μm long, continued by a dorsal tooth 6 μm high. The walls of protostoma possess cuticular teeth, two on each wall. There are ten cephalic setae (6 + 4), 12 μm and 8 μm respectively. The spiral amphids have four turns.

In males, the spicules are arched. Gubernaculum is similar in size to the spicules and its ventral (distal) edge is provided with teeth of different sizes. The caudal glands are well developed. The a.d. is 60-65 μm.

Sample data : 21-1 : 4 (UHM), 11 (LHM) ; 28 : 1 (LHS).

Geographic distribution : Chilean coast.

Remarks

The specimens are somewhat smaller than the original description given by WIESER (1954), but de Man's ratios are very similar.

The gubernaculum is not exactly the same, but the high similarity of the other characters leads us to consider the species as *P. austrospectabilis*.

It represents a new record for our country.

Praeacanthonchus punctatus (BASTIAN, 1865) MICOLETZKY, 1924
(Plate II, Fig. 5a-h)

Measurements : five males and five females, in μm.

Length of body : 2025 ; 2137 ; 1815 ; 2212 ; 2100 ; 2175 ; 2265 ; 2085 ; 2058 ; 1837.

Length of oesophagus : 225 ; 225 ; 195 ; 225 ; 225 ; 225 ; 225 ; 262 ; 244 ; 187.

Maximum width : 75 ; 75 ; 56 ; 75 ; 71 ; 94 ; 82 ; 94 , 75 ; 82.

Length of tail : 187 ; 172 ; 157 ; 206 ; 195 ; 169 ; 187 ; 187 ; 187 ; 150.

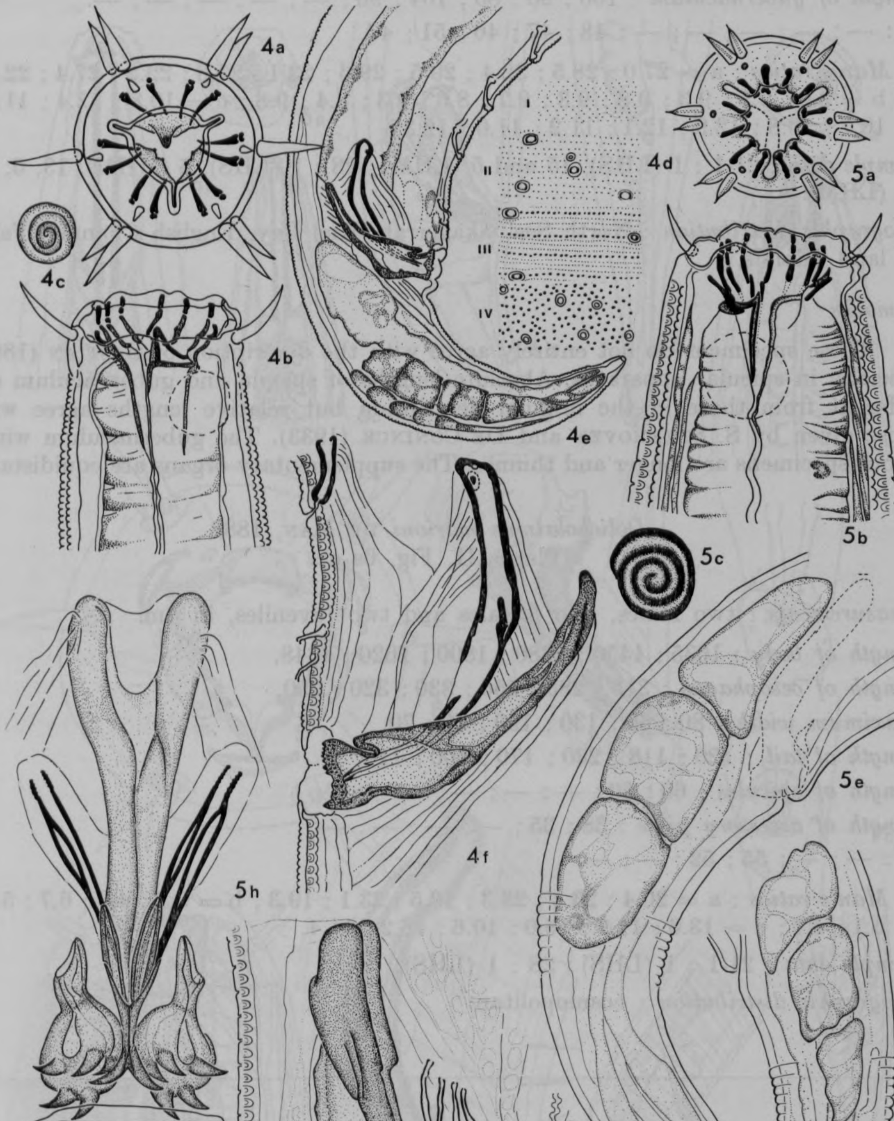
PLATE II

Paracanthonchus austrospectabilis Fig. 4a-f : a) head, apical view ; b) head, lateral view ; c) amphid ; d) cuticle : I. on head, at the top, II. on head, over buccal cavity, III. on the middle of the body, IV. over tail ; e) posterior end, general aspect ; f) spicules.

Praeacanthonchus punctatus Fig. 5a-h : a) head, apical view ; b) head, lateral view ; c) amphid ; d) cuticle : I. on head, II. on the middle of the body. III. on tail ; e) tail of male ; f) tail of female ; g) detail of spicules and gubernaculum, lateral view ; h) detail of spicules, ventral view.

Scales : A = 4e, 5e & f ; B = 4a-d & f, 2a-d, g & h.

PLATE II


4a
4c
4b
I
II
III
IV
4d
4e
5a
5b
5c
5e
4f
5h
5f
5g
I
II
III
5d
A 40μm
B 40μm

Length of spicules : 60 ; 44 ; 40 ; 60 ; 60 ; — ; — ; — ; — ; —.

Length of gubernaculum : 100 ; 90 ; 80 ; 104 ; 96 ; — ; — ; — ; — ; —.

V : — ; — ; — ; — ; — ; 48 ; 47 ; 46 ; 51 ; 47.

de Man's ratios : a = 27.0 ; 28.5 ; 32.4 ; 29.5 ; 29.6 ; 23.1 ; 27.6 ; 22.2 ; 27.4 ; 22.4 ; b = 9.0 ; 9.5 ; 9.3 ; 9.8 ; 9.3 ; 9.7 ; 8.6 ; 9.3 ; 8.4 ; 9.8 ; c = 10.8 ; 12.4 ; 11.6 ; 10.7 ; 10.8 ; 12.9 ; 12.1 ; 11.2 ; 11.0 ; 12.3.

Sample data : 21-1 : 1 (LHS), 15 and 5 (LHM) ; 28 : 1 (LHS), 5 (MHM), 13, 5, 19 (LHM).

Geographic distribution : North Sea, Skagerrak, Kiel Bay, English Channel, Falkland Islands.

Remarks

These specimens do not entirely agree with the description of Bastian (1865) specially in spicular apparatus. Absolute lengths of spicula and gubernaculum are different from those in the original description but relative lengths agree with those given by S. Stekhoven and De Coninck (1933). The gubernaculum wings in our specimens are longer and thinner. The supplementary organs are equidistant.

Dolicholaimus marioni de Man, 1888

(Plate III, Fig. 6a-e)

Measurements : two males, two females and two juveniles, in µm.

Length of body : 1635 ; 1450 ; 3680 ; 1800 ; 1620 ; 1348.

Length of oesophagus : 315 ; 285 ; 550 ; 330 ; 320 ; 290.

Maximum width : 80 ; 60 ; 130 ; 190 ; 70 ; 70.

Length of tail : 120 ; 118 ; 230 ; 170 ; 100 ; 118.

Length of spicules : 60 ; 60 ; — ; — ; — ; —.

Length of accessory piece : 38 ; 35 ; — ; — ; — ; —.

V : — ; — ; 55 ; 52 ; — ; —.

de Man's ratios : a = 20.4 ; 23.4 ; 28.3 ; 19.5 ; 23.1 ; 19.3 ; b = 5.2 ; 4.9 ; 6.7 ; 5.5 ; 5.1 ; 4.7 ; c = 13.6 ; 11.9 ; 16.0 ; 10.6 ; 16.2 ; 11.4.

Sample data : 21-1 : 1 (LHS) ; 28 : 1 (LHS).

Geographic distribution : cosmopolitan.

PLATE III

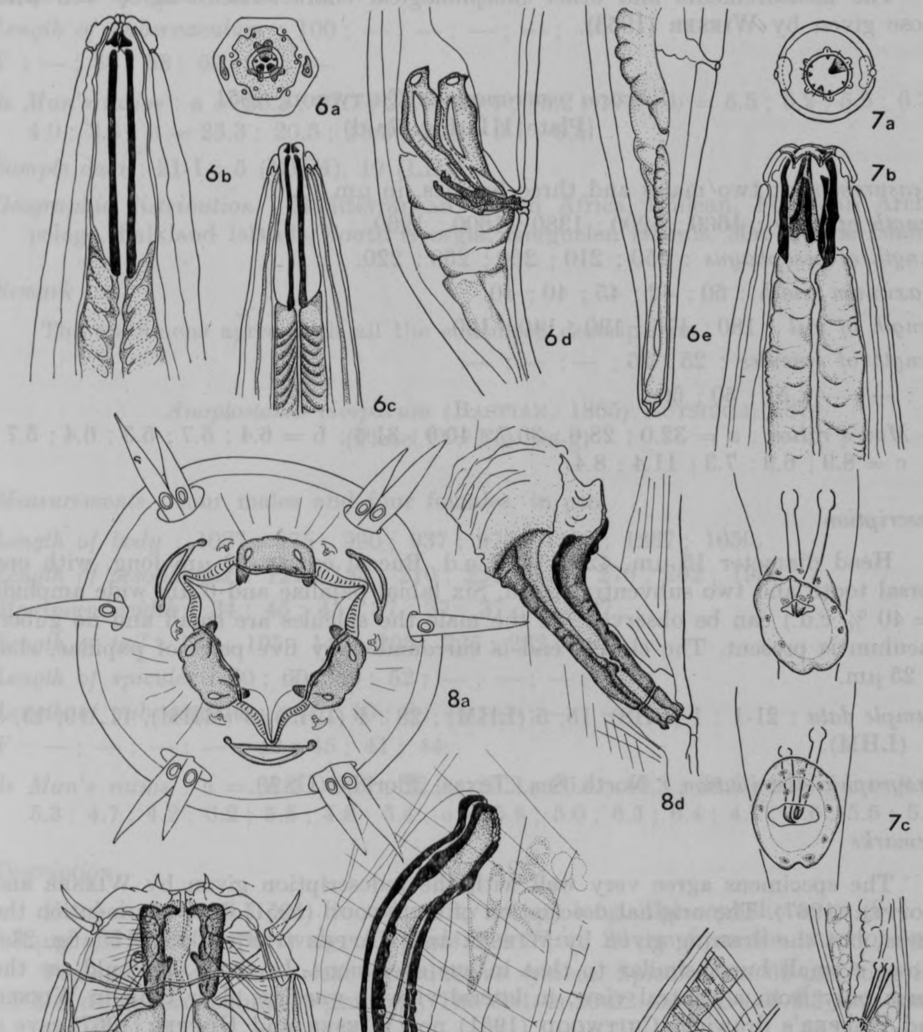
Dolicholaimus marioni Fig. 6a-e : a) head, apical view ; b) head, lateral view (stylet protruded) ; c) head, lateral view ; d) detail of spicules and gubernaculum ; e) tail of male.

Viscosia macramphida Fig. 7a-d : a) head, apical view ; b) head, lateral view ; c) spicules, ventral view ; d) tail.

Enoplus michaelseni Fig. 8a-e : a) head, apical view ; b) head, lateral view ; c) posterior end, male ; d) detail anterior supplements ; e) detail of spicules and gubernaculum.

Scales : A = 8c ; B = 6b-e, 7d, 8d-e ; C = 6a, 7a-c, 8a.

PLATE III



Remark

The measurements and other morphological characteristics agree well with those given by WIESER (1953).

Viscosia macramphida CHITWOOD, 1951
(Plate III, Fig. 7a-d)

Measurements : two males and three females, in μm.

Length of body : 1600 ; 1200 ; 1380 ; 1600 ; 1260.

Length of oesophagus : 250 ; 210 ; 260 ; 250 ; 220.

Maximum width : 50 ; 42 ; 45 ; 40 ; 40.

Length of tail : 180 ; 175 ; 190 ; 140 ; 150.

Length of spicules : 25 ; 25 ; — ; — ; —.

V : — ; — ; 51 ; 50 ; 60.

de Man's ratios : a = 32.0 ; 28.6 ; 30.7 ; 40.0 ; 31.5 ; b = 6.4 ; 5.7 ; 5.3 ; 6.4 ; 5.7 ; c = 8.9 ; 6.9 ; 7.3 ; 11.4 ; 8.4.

Description

Head diameter 15 μm, 42.8 % of o.d. Buccal cavity 20 μm long, with one dorsal tooth and two subventral teeth. Six labial papillae and 6 μm wide amphids (= 40 % c.d.) can be observed. In the male the spicules are small and no gubernaculum is present. The cloacal end is surrounded by five pairs of papillae, cl.d. is 25 μm.

Sample data : 21-1 : 1 (LHS), 15, 5 (LHM) ; 28 : 1 (LHS), 5 (MHM), 11, 19, 13, 5 (LHM).

Geographic distribution : North Sea, Texas, Florida (USA).

Remarks

The specimens agree very well with the redescription given by WIESER and HOPPER (1967). The original description of CHITWOOD (1951) does not mention the bursa, but the drawing given by WIESER and HOPPER (1967, Plate XII, fig. 23c) shows a small bursa similar to that in our specimens. In these we could see the bursa only from a ventral view, in lateral view it was less clear than in WIESER and HOPPER's drawing. CHITWOOD (1951) nor WIESER and HOPPER (1967) gave a drawing in ventral view. So, it is impossible to compare exactly.

This species is a new record for our country and for the Southern Hemisphere.

Enoplus michaelseni v. LINSTOW, 1896
(Plate III, Fig. 8a-e)

Measurements : one male, three females and two juveniles, in μm.

Length of body : 6060 ; 7190 ; 5850 ; 5080 ; 1820 ; 1430.

Length of oesophagus : 1100 ; 1160 ; 1060 ; 820 ; 450 ; 430.

Maximum width : 200 ; 260 ; 240 ; 200 ; 120 ; 80.

Length of tail : 260 ; 350 ; 320 ; 300 ; 200 ; 150.

Length of spicules : 220 ; — ; — ; — ; — ; —.

Length of gubernaculum : 100 ; — ; — ; — ; — ; —.

V : — ; 56 ; 58 ; 59 ; — ; —.

de Man's ratios : a = 30.3 ; 27.7 ; 24.4 ; 25.4 ; 15.2 ; 17.9 ; b = 5.5 ; 6.2 ; 5.5 ; 6.2 ; 4.0 ; 3.3 ; c = 23.3 ; 20.5 ; 18.3 ; 16.9 ; 9.1 ; 9.5.

Sample data : 21-1 : 5 (MHM), 19 (LHM).

Geographic distribution : Mediterranean, South Africa, Chilean, Fueguian Archipelago, Falkland Islands, South Georgia, Kerguelen Islands, Mac Quarie Island.

Remark

The specimens agree with all the consulted descriptions.

Anoplostoma viviparum (BASTIAN, 1865) BÜTSCHLI, 1874

(Plate IV, Fig. 9a-g)

Measurements : four males and four females, in µm.

Length of body : 1087 ; 975 ; 990 ; 937 ; 975 ; 1492 ; 1267 ; 1050.

Length of oesophagus : 127 ; 184 ; 210 ; 221 ; 157 ; 270 , 262 ; 195.

Maximum width : 34 ; 45 ; 45 ; 37 ; 37 ; 37 ; 45 ; 37.

Length of tail : 187 ; 195 ; 146 ; 206 ; 225 ; 232 ; 187 ; .

Length of spicules : 60 ; 60 ; 60 ; 52 ; — ; — ; — ; —.

Length of gubernaculum : 10 ; 10 ; 8 ; — ; — ; — ; — ; —.

V : — ; — ; — ; — ; 42 ; 45 ; 41 ; 44.

de Man's ratios : a = 32.0 ; 21.7 ; 22.0 ; 25.3 ; 26.4 ; 40.3 ; 28.2 ; 28.4 ; b = 8.6 ; 5.3 ; 4.7 ; 4.2 ; 6.2 ; 5.5 ; 4.8 ; 5.4 ; c = 5.8 ; 5.0 ; 6.3 ; 6.4 ; 4.7 ; 6.6 ; 5.5 ; 5.6.

Description

Head diameter 6-7 µm. Buccal cavity 10 µm long. The cephalic setae (6 + 4) 8-9 µm and 6 µm respectively. Amphids 3 × 5 µm, 20 µm from the anterior end.

Females have symmetrical reproductive system. Spicules are 60 µm long i.e. 2.9-3 cl.d., gubernaculum 10 µm long. The cl.d. is 20-22 µm and tail 9.3 cl.d. long.

Sample data : 21-1 : 1 (LHS) ; 28 : 13 (LHM).

Geographic distribution : cosmopolitan.

Remarks

These specimens show some differences with the description given by BASTIAN (1865). De Man's ratio « c » is smaller but tail length in cl.d. is similar to the other descriptions that have been consulted. Also the distance of the vulva from the anterior end is different.

In males, the spicules are longer.

A. viviparum is a new record for our country.

Anoplostoma camus WIESER, 1953
(Plate IV, Fig. 10a-e)

Measurements : one male and two juveniles, in µm.

Length of body : 1050 ; 930 ; 900.
Length of oesophagus : 232 ; 187 ; 195.
Maximum width : 34 ; 37 ; 30.
Length of tail : 82 ; 75 ; 82.
Length of spicules : 64 ; — ; —.

de Man's ratios : a = 30.9 ; 25.3 ; 30.0 ; b = 4.5 ; 5.0 ; 4.6 ; c = 12.8 ; 12.4 ; 11.0.

Description

Cephalic diameter 7 µm. Buccal cavity 13 µm long. The (6 + 4) cephalic setae measure 8 and 5 µm respectively. The excretory gland is 23 µm from the anterior end. Cl.d. is 20 µm ; the spicules are 62 µm (3 cl.d.) and the gubernaculum 11 µm (0.5 cl.d.).

Sample data : 21-1 : 7 (LHM) ; 28 : 5 (MHM), 19 (LHM).

Geographic distribution : Chilean coast.

Remarks

The specimens agree with the description given by WIESER (1954).

It represents a new record for our country.

Paramonohystera subgen. *Paramonohystera proteus* WIESER, 1956
(Plate V, Fig. 11a-e)

Measurements : four males and one female, in µm.

Length of body : 900 ; 900 ; 862 ; 900 ; 975.
Length of oesophagus : 187 ; 184 ; 169 ; 150 ; 187.
Maximum width : 37 ; 22 ; 34 ; 45 ; 56.
Length of tail : 94 ; 105 ; 79 ; 82 ; 112.
Length of spicules : 120 ; 120 ; 100 ; 116 ; —.
Length of gubernaculum : 20 ; 20 ; 20 ; 24 ; —.
V : — ; — ; — ; — ; 50.1.

de Man's ratios : a = 24.3 ; 40.9 ; 25.3 ; 20.0 ; 17.4 ; b = 4.8 ; 4.9 ; 5.1 ; 6.0 ; 5.2 ; c = 9.6 ; 8.6 ; 10.9 ; 11.0 ; 8.7.

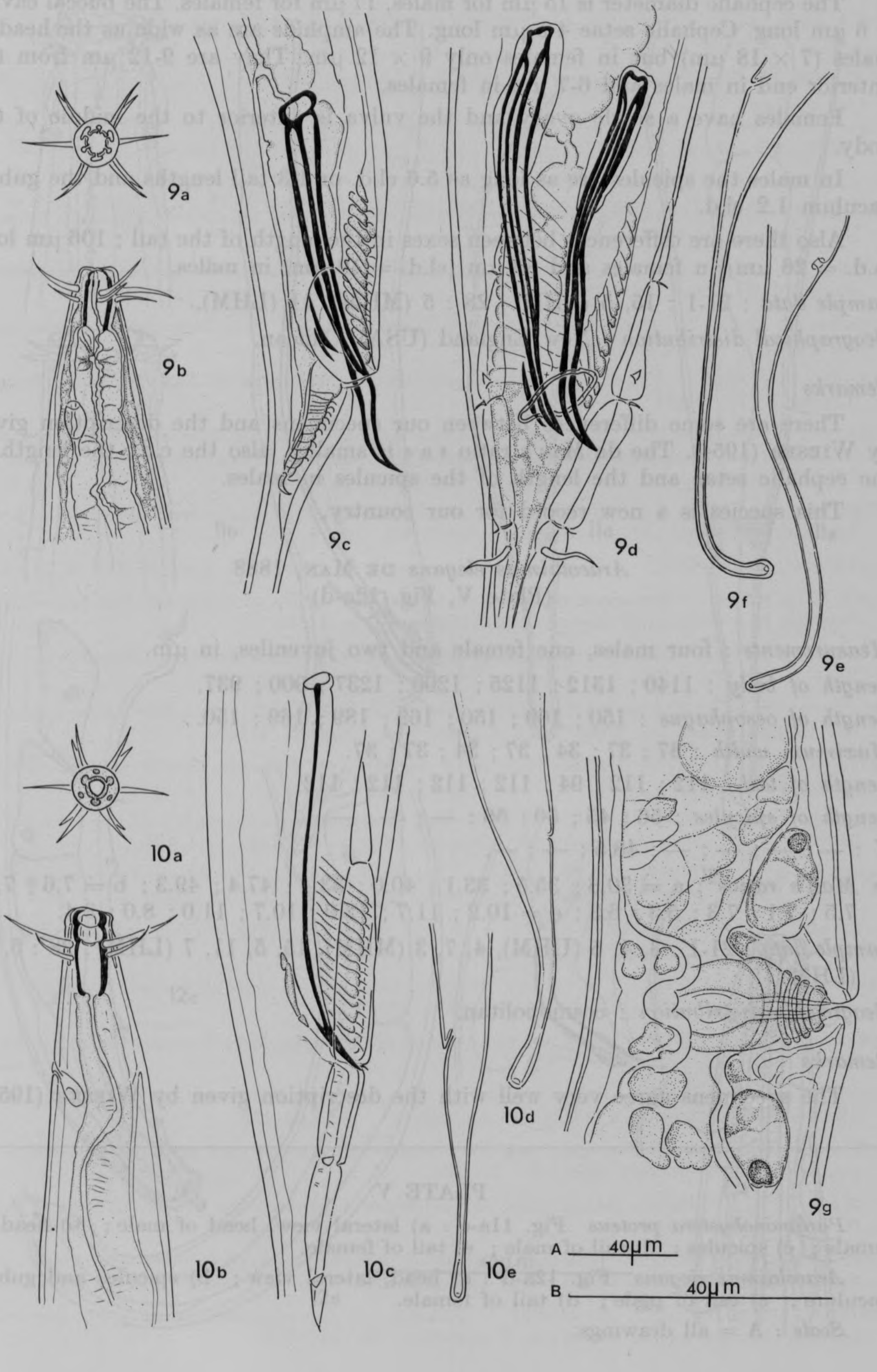
PLATE IV

Anoplostoma viviparum Fig. 9a-g : a) head, apical view ; b) head, lateral view ; c) spicules, lateral view ; d) spicules, ventral view ; e) tail of male ; f) tail of female ; g) detail of vulva.

Anoplostoma camus Fig. 10a-e : a) head, apical view ; b) head, lateral view ; c) spicules, lateral view ; d) tail of male ; e) tail of female.

Scales : A = 9e-f, 10d-e ; B = 9a-d, 9g, 10a-c.

PLATE IV



Description

The cephalic diameter is 15 μm for males, 17 μm for females. The buccal cavity is 6 μm long. Cephalic setae 4-5 μm long. The amphids are as wide as the head in males (7 × 18 μm) but in females only 9 × 12 μm. They are 9-12 μm from the anterior end in males and 6-7 μm in females.

Females have a single ovary and the vulva is anterior to the middle of the body.

In males the spicules are as long as 5.6 cl.d. or 1.3 tail lengths and the gubernaculum 1.2 cl.d.

Also there are differences between sexes in the length of the tail : 106 μm long (a.d. = 26 μm) in females and 80 μm (cl.d. = 19 μm) in males.

Sample data : 21-1 : 15, 5 (LHM) ; 28 : 5 (MHM), 11 (LHM).

Geographical distribution : New England (USA), Chilean.

Remarks

There are some differences between our specimens and the description given by Wieser (1954). The de Man's ratio « a » is smaller, also the c.d., the length of the cephalic setae and the length of the spicules in males.

This species is a new record for our country.

Araeolaimus elegans de Man, 1888
(Plate V, Fig. 12a-d)

Measurements : four males, one female and two juveniles, in μm.

Length of body : 1140 ; 1312 ; 1125 ; 1200 ; 1237 ; 900 ; 937.

Length of oesophagus : 150 ; 169 ; 150 ; 169 ; 189 ; 169 ; 150.

Maximum width : 37 ; 37 ; 34 ; 37 ; 34 ; 37 ; 37.

Length of tail : 112 ; 112 ; 94 ; 112 ; 112 ; 112 ; 112.

Length of spicules : 56 ; 45 ; 56 ; 56 ; — ; — ; —.

V : — ; — ; — ; — ; 48.5 ; — ; —.

de Man's ratios : a = 30.8 ; 35.5 ; 33.1 ; 40.0 ; 33.4 ; 47.4 ; 49.3 ; b = 7.6 ; 7.8 ; 7.5 ; 7.1 ; 7.3 ; 5.3 ; 6.3 ; c = 10.2 ; 11.7 ; 12.0 ; 10.7 ; 11.0 ; 8.0 ; 8.4.

Sample data : 21-1 : 3, 4, 5 (UHM), 4, 7, 3 (MHM), 15, 5, 11, 7 (LHM) ; 28 : 5, 19 (LHM).

Geographic distribution : cosmopolitan.

Remarks

The specimens agree very well with the description given by Wieser (1956).

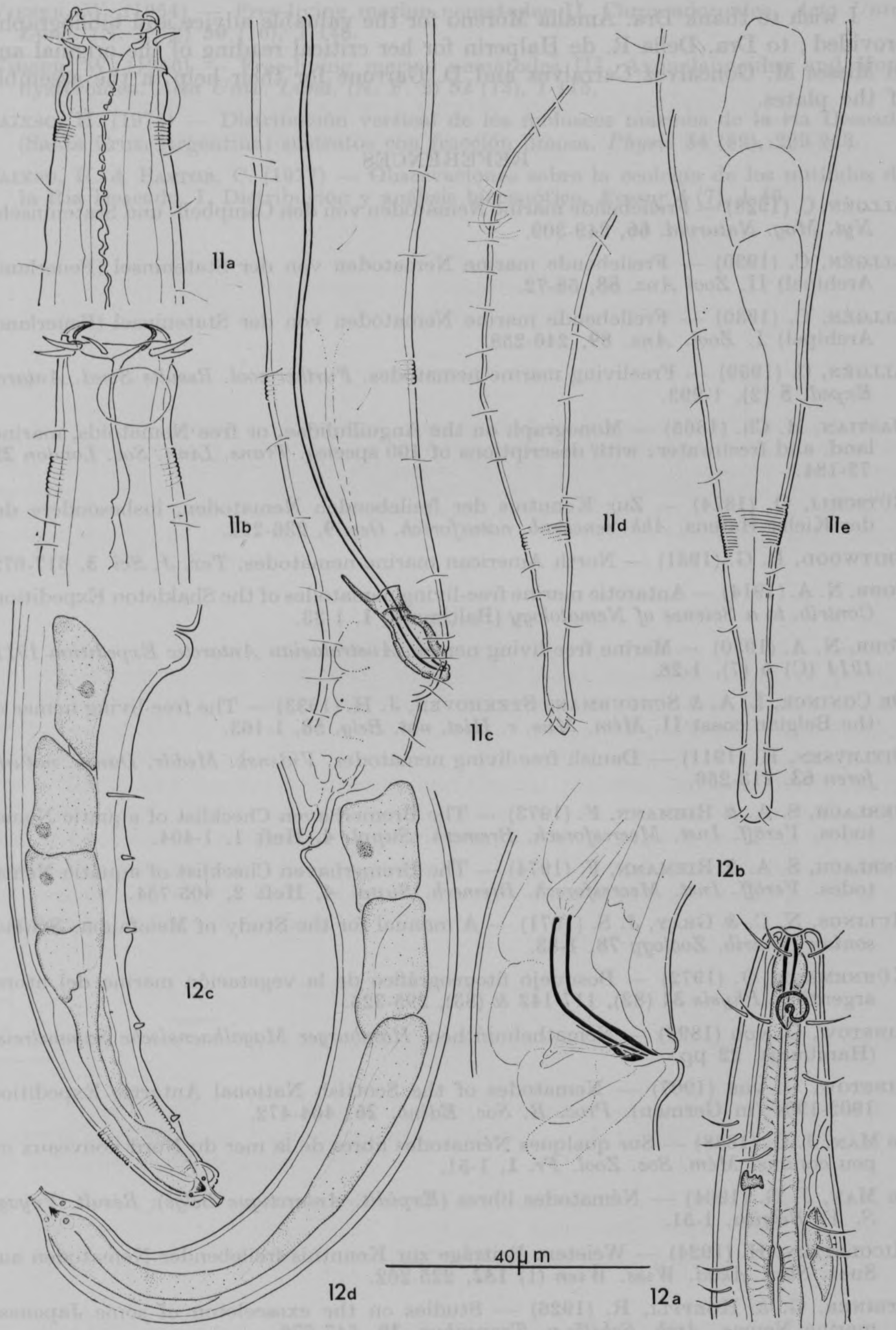
PLATE V

Paramonohystera proteus Fig. 11a-e : a) lateral view, head of male ; b) head of female ; c) spicules ; d) tail of male ; e) tail of female.

Araeolaimus elegans Fig. 12a-d : a) head, lateral view ; b) spicules and gubernaculum ; c) tail of male ; d) tail of female.

Scale : A = all drawings.

PLATE V



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BENTHIC NEMATODES FROM THE PACIFIC COAST WITH SPECIAL REFERENCE TO THE CYATHOLAIMIDS

by

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ABSTRACT

Over thirty genera of free-living nematodes from seventeen families have been found during a survey of the benthic meiofauna of the Pacific Coast near Vancouver. Their distribution appears to be influenced by the quantity of organic matter and associated bacteria in the sediment. The taxonomy of the Cyatholaimidae will be examined, especially those members of the Cyatholaiminae. The use of light and scanning electron microscope observations of pores and punctuations as taxonomic aids within this family will be discussed.

INTRODUCTION

We report on part of a study of the free-living nematode fauna of coastal British Columbia. Until now, the only comprehensive studies on the free-living marine nematodes of the west coast of North America are those from : Puget Sound, Washington (WIESER, 1959), Oregon (MURPHY, 1961), Northern California (CHITWOOD, 1960), and Southern California and Central America (ALLGÉN, 1947, 1951). Only two reports are available for the Canadian Pacific coast, namely, the redescription of *Oncholaimus vesicarius* (NELSON et al., 1971) and the description of a new species, *Enoplus anisospiculus* (NELSON et al., 1972). Since no comprehensive studies are available for the West Coast of Canada, a primary purpose of our study is to investigate the nematode fauna of this area.

HABITAT DESCRIPTION

Nematodes were collected from three different sites in Greater Vancouver (Fig. 1), namely :

(i) Iona Island : a tidal flat with a gently sloping beach in the estuary of the Fraser River, south of Vancouver, with jetties on either side of it that minimize the influence of fresh water.

(ii) Stanley Park : a sandy beach at the mouth of Burrard Inlet which contains the dock facilities of a major port. Its slope is somewhat steeper than the beach at Iona Island and it is heavily used for recreational and educational purposes.

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(iii) Belcarra Park : a small steeply sloping beach close to a bed of eel grass (*Zostera* sp.) at the mouth of a deep water fjord.

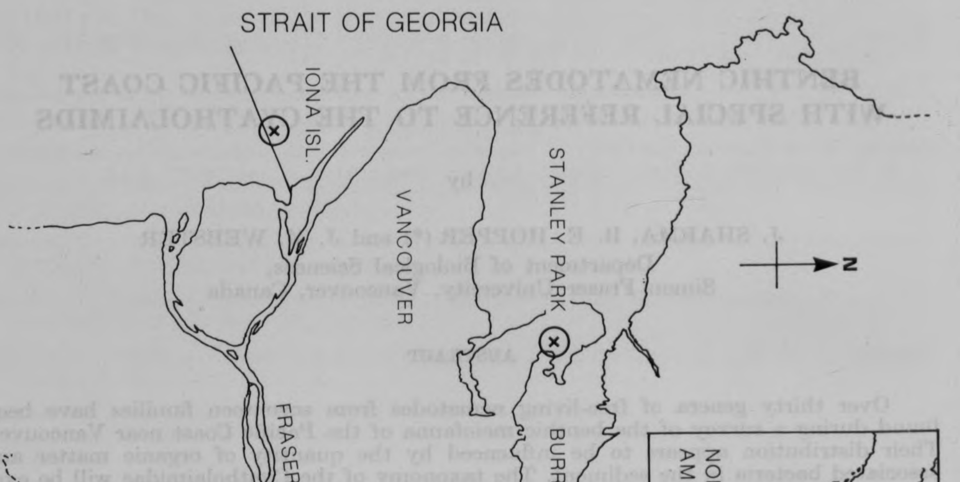

Fig. 1. — Map of Greater Vancouver, British Columbia showing the location of three nematode collection sites.

The sediment at Iona Island is well sorted (as determined by dry sieving) with most of it falling within a narrow range of grain sizes. Both Stanley Park and Belcarra Park sites, however, have poorly sorted sediments with a wide range of grain sizes.

A quantitative estimate of the detrital material in the beach sediments was obtained by measuring with a CHN analyzer the per cent of carbon present. It was lowest in the Iona Island sediments (0.52 %) and highest in the poorly sorted sediments of Belcarra Park (2.35 %).

The degree of bacterial activity in the sediments was assessed by determining the heterotrophic activity of the bacteria. This was done by measuring the amount of radiolabelled glucose the bacteria take up. It was lowest in the Iona Island sediments (1.6×10^4 DPM) and highest in Belcarra Park sediments (1.2×10^5 DPM). Hence, preliminary evidence suggests that there is higher bacterial activity in the more organic sediments at the Belcarra Park site than in the well washed, relatively clean Iona Island site.

ECOLOGICAL INVESTIGATIONS

Sediment samples were taken at about mid-tide level at each of the three sites by a hand-held plexiglass corer. The upper 6 cm of the core were examined in 2 cm sections and nematodes were extracted from each section by sieving and centrifugation.

Nematodes representing 20 families and 40 genera (Table I) were recovered from the sediments. Some families that were well represented at Belcarra Park and Stanley Park were absent from all samples from Iona Island. The total number of nematodes in the samples at Iona Island is much lower than that at either of the other two sites. Preliminary observations suggest that the nematodes differ in their distribution at the three sites.

TAXONOMIC CONSIDERATIONS

A prominent group of nematodes found in this study is the order Chromadorida which is represented by species from all its families, namely, Comesomatidae, Cyatholaimidae, Choanolaimidae, Chromadoridae, Desmodoridae. The Cyatholaimids are represented by three *Marylynnia* species two of which were collected intertidally and one subtidally. Although on initial observation they all appeared very similar in having a prominent dorsal tooth and multispiral amphid, they differ in some features and especially in the pattern of cuticular pores.

The « pores » referred to here appear, under light microscopy, as circles of varying sizes and shapes amongst the punctations which appear as dots in several Chromadorids. Little attention has been given to the type and number of pores in relation to species identification. One reason for this lack of utilization in taxonomy could be the difficulty of distinguishing the different types at the normal resolution of the light microscope. The lack of complete data on the pores has minimized their inclusion in standard taxonomic descriptions. Hence, their value in taxonomy has not been fully realized. The scanning electron microscope is particularly useful in ascertaining the relative position and distribution of the pores and also their association with the cuticular surface.

Since the earliest record of pores by Bastian in 1865, several taxonomic papers have recorded the presence of pores (see Table II). Bastian (1865) recorded their presence in various nematode species and the differences he noted suggest that the number of pores varies with species. Chitwood and Chitwood (1950) described pores, in both the Enoplida and Chromadorida, as the openings of two sublateral rows of unicellular glands situated in the lateral chords. They also noted that these glands occur only in the Aphasmidea (= Adenophorea). Such pores are not confined to the Cyatholaimidae but have been described also from the Eurystominidae (Hopper, 1970) and the Desmodoridae (Hopper and Cefalu, 1970). Schuurmans,

TABLE I

Nematode genera present at the three collection sites in the Greater Vancouver Area

		Iona Island	Stanley Park	Belcarra Park
Araeolaimida				
Leptolaimidae	*Leptolaimus*	—	+	+
Axonolaimidae	*Araeolaimus*	—	+	+
	Axonolaimus	—	+	+
	Odontophora	—	+	+
	Parascolaimus	+	+	+
Monhysterida				
Siphonolaimidae	*Siphonolaimus*	—	+	+
Linhomoeidae	*Desmolaimus*	—	+	+
	Metalinhomoeus	—	—	+
	Tershellingia	+	+	+
	Eleutherolaimus	—	+	+
	Didelta	—	+	+
	Linhomoeus	—	+	+
Monhysteridae	*Monhystera*	—	—	+
	Steineria	—	+	+
	Theristus	+	+	+
Sphaerolaimidae	*Sphaerolaimus*	—	—	+
Chromadorida				
Comesomatidae	*Sabatieria*	+	+	+
Chromadoridae	*Ethmolaimus*	—	—	+
	Chromadorina	—	+	+
	Euchromadora	—	—	+
	Neochromadora	+	+	+
	Spilophorella	—	—	+
Cyatholaimidae	*Paracanthoncus*	—	—	+
	Cyatholaimus	—	—	+
	Marylynnia	+	+	+
Choanolaimidae	*Choanolaimus*	—	—	+
Enoplida				
Tripyloididae	*Bathylaimus*	—	+	+
	Paratripyloides	—	—	+
	Tripyloides	+	+	+
Oxystominidae	*Oxystomina*	—	—	+
Lauratonematidae	*Lauratonema*	—	—	+
Anticomidae	*Anticoma*	—	—	+
Enoplidae	*Oxyonchus*	+	+	+
	Mesacanthion	—	—	+
Oncholaimidae	*Oncholaimus*	+	+	+
Encheliidae	*Eurystomina*	—	—	+
	Symplocostoma	—	—	+

STEKHOVEN and TEUNISSEN (1938) recorded the distribution and number of pores in *Plectus granulosus*. However, the Cyatholaimidae is the only family of marine nematodes in which hypodermal pores have been consistently recorded and in which their structure has been the subject of investigation.

TABLE II

A representative chronological list of records that describe the presence of pores in free-living marine nematodes

1. 1865, BASTIAN	fine capillary canals ; lateral integumental pores
2. 1890, DE MAN	round pores
3. 1898, COBB	longitudinal rows of circles in the lateral regions
4. 1917, COBB	longitudinal series of repetitive organs in lateral fields
5. 1918, FILIPJEV	row of circular pores along lateral lines
6. 1933, DE CONINCK and SCHUURMANS STEKHOVEN	one or more rows of finer pointlets in dorsal and ventral fields
7. 1950, CHITWOOD and CHITWOOD	lateral hypodermal glands
8. 1954, WIESER	conspicuous pores
9. 1967, WIESER and HOPPER	longitudinal series of hypodermal pores
10. 1970, VITIELLO	pore complexes described in five genera
11. 1971, WARWICK	two types of lateral pores ; start anterior to excretory pores and extend 2/3 of esophageal length
12. 1972, HOPPER	longitudinal rows pore complexes
13. 1972, HOPPER	pore complexes in *Marylynnia* sp. and *Longicyatholaimus* sp. distinguished
14. 1972, HOPPER and CEFALU	longitudinal rows of pore complexes

INGLIS (1963) was the first person to describe cuticular pore structures in detail and he compared them to the « campaniform-type » organs which act as proprioceptors in insects. He described two types of pores : an ovoid type with a transverse sheet of cuticle (type-1) and a circular type with a raised central dome (type-2). Since then the two types of pores have been referred to as hypodermal pores and lateral modified punctations (LMP's) respectively by several authors. Hypodermal pores, which appear as pores with a transverse slit, occur in up to 12 longitudinal rows around the circumference of the body. The most prominent are the two sublateral rows situated in the region of the lateral chords. Normally, the hypodermal pores in these rows are spaced uniformly throughout the body length. There are fewer longitudinal rows of LMP's, each of which appear as pores placed between two punctations, and generally, only a single row of LMP's are present in each lateral aspect. However, their distribution within this row is highly variable between species. WARWICK (1971) refers to these two types of pores as type-a and type-b, respectively.

Although the presence of the two types of pores has been confirmed by several authors, a different interpretation of pore structure resulted from the ultrastructure studies of WRIGHT and HOPE (1968). They describe the pore as a complex consisting of : a shallow depression in the outer cuticle, a slit-like pore extending through the deeper cuticular layers into an underlying hypodermal cell, and a ring or collar-like development of dense material in the middle cuticle layer. They introduced the term « pore complex » for the type-1 pore described by INGLIS because several components of the cuticle contribute to the image of a circle with transverse bar that is seen on the cuticle surface with a light microscope.

The function of the pore complex is not clear. CHITWOOD and CHITWOOD (1950) used the term « lateral hypodermal glands » to describe the structures beneath these pores in the Enoplida and Chromadorida. DE MAN (1889) drew glands in some of his figures of *Paracanthonchus ocellatus* BASTIAN and showed their relationship to pores. SCHUURMANS STEKHOVEN (1935) refers to pores in relation to « skin glands ». Nevertheless, only the term hypodermal has been retained by WRIGHT and HOPE (1968) because the pores are not restricted to a lateral position and their function as glandular openings has not been demonstrated.

Although various authors have noted the presence of hypodermal pore complexes and various names have been assigned to them, the possible taxonomic significance of their kinds and numbers has been ignored. In distinguishing the species of a Canaloid copepod, *Eucalanus*, FLEMINGER (1973) showed that the distribution pattern and number of integumental organs, which include sensilla and glandular pores, are of taxonomic significance. The distribution of hypodermal pore complexes and modified punctations may be equally important in the taxonomy of some nematode groups. The importance of such meristic or countable characters has been emphasized in taxonomy (MAYR, 1969), because in statistical usage, they are discrete variables, and the fact that they can only take on certain values makes them taxonomically more reliable.

The pore patterns for each of the three *Marylynnia* species in our collection are very distinctive (Fig. 2). The arrangement of the hypodermal pore complexes on the cuticle in each of the three species is constant among adults and juveniles and conforms with the general description given above. The LMP's show greater interspecific variation in their cuticular arrangement than do the hypodermal pores. However, the arrangement is consistent within a species.

Marylynnia sp. 1 has a cluster of LMP's behind the head extending for about 100 µm with 25-35 units in the cluster. There is no discernible pattern within the cluster, although the placement of the LMP's is similar in all specimens examined. A row of 10-12 LMP's occurs in the preanal-caudal region of both sexes. The male lacks further LMP's but the female has short rows containing 3 to 4 pores located a short distance anterior and posterior to the vulvar region.

Marylynnia sp. 2 has a row of 15-20 anteriorly placed LMP's extending about one-third the esophageal length. 8-10 LMP's occur in the caudal region and none were found elsewhere on the body.

In *Marylynnia* sp. 3 the LMP's are not clustered at the anterior end. Instead, two rows of hypodermal pores occur laterally starting 46-73 µm from the anterior end, while the LMP's start one-third of the way down the esophageal region and continue the length of the body.

All three species of *Marylynnia* had pores and modified punctations arranged in varying densities over all the body and therefore data was collected (Table III) so as to differentiate between the species on the basis of their pores. The following observations were made : (i) The distance behind the head of the first hypodermal pore was constant for a given species. (ii) The number of hypodermal pores and LMP's in the esophageal region was constant for a given species. (iii) The number

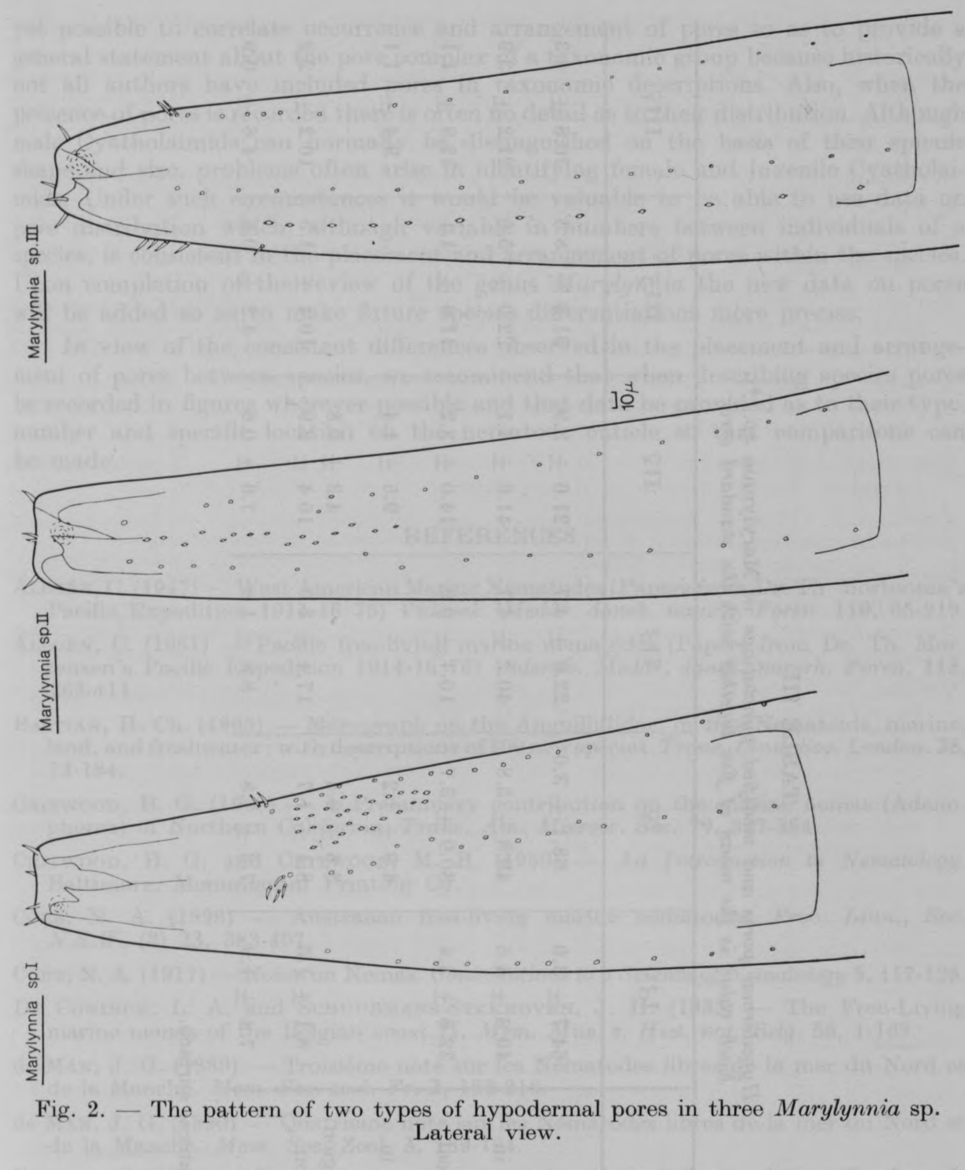

Fig. 2. — The pattern of two types of hypodermal pores in three *Marylynnia* sp. Lateral view.

of pores and LMP's in the tail region were constant for a given species but often difficult to ascertain because the tails of fixed nematodes were frequently curled. (iv) Counting all pores and LMP's over the body is very time consuming, hence the number of pores and LMP's in a row were counted (a) from the base of the esophagus to the anterior end, (b) 15.5 μm on either side of the vulva and (c) on the tail, (v) Varying patterns of distribution may sometimes require other measurements to be made in order to differentiate between some species.

Hopper (1972) defined *Marylynnia* sp. as having a greater number of hypodermal pore complexes and LMP's than *Longicyatholaimus* sp. However, it is not

TABLE III

Hypodermal pores and modified punctations in Marylynnia *sp.* (*).
Each value is the mean of five together with the standard error

	I♂	I♀	II♂	II♀	III♂	III♀
Distance behind head of first pore (μm)	64.7 ± 3.6	68.1 ± 3.0	22.6 ± 4.7	21.6 ± 3.9	31.3 ± 8.3	30.8 ± 5.3
No. of hypodermal pores in esophageal region	49.8 ± 4.5	49.8 ± 5.8	40.2 ± 4.7	41.6 ± 4.1	22.0 ± 5.0	21.2 ± 3.9
No. of LMP's in esophageal region	32.6 ± 3.4	30.0 ± 3.7	10.4 ± 0.9	14.0 ± 3.2	11.6 ± 1.1	12.8 ± 1.1
No. of hypodermal pores in vulvar region		4.9 ± 1.2		9.5 ± 1.4		9.4 ± 1.1
No. of LMP's in vulvar region		3.8 ± 0.4		4.2 ± 0.8		
No. of hypodermal pores on tail	8.1 ± 1.5	8.1 ± 1.7	17.4 ± 3.0	16.4 ± 2.9	10.4 ± 1.5	10.2 ± 2.2
No. of LMP's on tail	7.4 ± 1.9	7.2 ± 1.8	8.8 ± 1.8	7.6 ± 0.6	4.2 ± 0.5	4.6 ± 0.9

(*) As viewed from lateral surface.

yet possible to correlate occurrence and arrangement of pores so as to provide a general statement about the pore complex of a taxonomic group because historically not all authors have included pores in taxonomic descriptions. Also, when the presence of pores is recorded there is often no detail as to their distribution. Although male Cyatholaimids can normally be distinguished on the basis of their spicule shape and size, problems often arise in identifying female and juvenile Cyatholaimids. Under such circumstances it would be valuable to be able to use data on pore distribution which, although variable in numbers between individuals of a species, is consistent in the placement and arrangement of pores within the species. Upon completion of the review of the genus *Marylynnia* the new data on pores will be added so as to make future species differentiations more precise.

In view of the consistent differences observed in the placement and arrangement of pores between species, we recommend that when describing species pores be recorded in figures wherever possible and that data be provided as to their type, number and specific location on the nematode cuticle so that comparisons can be made.

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OCCURRENCE AND TAXONOMICAL SIGNIFICANCE OF ADDITIONAL CEPHALIC SETAE IN SOME LINHOMOEIDAE (NEMATODA)

by

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ABSTRACT

The cephalic sensory structures, papillae and setae, were studied in five species of *Paralinhomoeus* (Linhomoeidae) by light and scanning electron microscopy. A basic cephalic pattern, six labial papillae and ten cephalic setae, was characteristic of all young juveniles. Additional cephalic setae were observed in adults of four species, most frequently in males, giving rise to a variation within species or a sexual dimorphism. The wide-spread occurrence and great variation in number of additional cephalic setae have to be considered before using the number of cephalic setae as a taxonomical character within *Paralinhomoeus* and related genera.

On the basis of present knowledge the delimitation of some genera within Linhomoeinae is doubtful and the genera *Perilinhomoeus* and *Anticyclus* are to be synonymized with *Paralinhomoeus*.

I. INTRODUCTION

Our present classification of the free-living marine nematodes is based almost entirely on morphological characters. As the number of recorded species and genera increases, very minute structural differences are often used to delimit different taxa. However, characters differ in their usefulness for classification and also in their contribution to facilitate proper identification.

An important character in nematode taxonomy is the number and position of cephalic setae. The occurrence of additional setae in the cephalic circle in some linhomoeids and the observed variation in number of these setae, may, as described below, illustrate the difficulties involved in using this particular character within the Linhomoeidae.

Initially only a restricted number of specimens of two closely related species of *Paralinhomoeus*, *P. lepturus* (DE MAN, 1907) and *P. intermedius* (ALLGÉN, 1929), were available for examination. In both species the males were found to differ from juveniles and females regarding the number of cephalic setae. Since the original material had been collected in sediment with pronounced oxygen deficiency, the possibility could not be excluded that the observed variation reflected local populations living under strong environmental stress. Consequently, additional material from other geographical areas was obtained, which included a further three species.

Misinterpretation and failure to observe certain structures cannot be excluded when light microscopy is used to analyse the number and position of the minute cephalic structures. Therefore, in addition to common *en face* preparations, material was examined by scanning electron microscopy which has the advantages, besides increased resolution and depth of field, that the nematodes can be tilted and rotated during examination, allowing observation from the most suitable angles.

The comparative studies presented at the symposium in Ghent on structures other than the cephalic setae will be published separately.

II. MATERIAL AND METHODS

Specimens of five species of *Paralinhomoeus* (Linhomoeidae, Nematoda) were studied. Four of them are referred to species described earlier (Tab. 1). They were collected in the Gullmar Fjord on the west coast of Sweden (species nos. II, III, and V), and in the northern part of the Øresund in the vicinity of Helsingør, Denmark (species nos. I, III, and V). The fifth species was collected on the coast of Bermuda by Professor S. A. Gerlach. It is a new species and will be described elsewhere. The nomenclature used in this paper follows GERLACH & RIEMANN (1973).

TABLE I

Species and number of specimens studied by light microscopy (LM) and scanning electron microscopy (SEM)

	LM			SEM		
	juv	♀	♂	juv	♀	♂
I. *Paralinhomoeus ilenensis* (ALLGÉN, 1933)	2	5	5			
II. *P. lepturus* (DE MAN, 1907)	34	46	40	9	28	42
III. *P. intermedius* (ALLGÉN, 1929)	9	34	28	9	20	22
IV. *Paralinhomoeus n. sp.*	37	8	3	5	2	
V. *P. cf strandibrevicaudatus* (ALLGÉN, 1934)	5	4	4	6	9	12

Preparation for light microscopy (LM). Some of the living nematodes were killed and fixed in cold 4 % neutral formaldehyde in sea water. In order to make preparations for LM and SEM (see below) suitable for comparison a number of nematodes were fixed in ice-cold 4.5 % glutaraldehyde in a solution of 0.2 mol/l cacodylate buffer and filtered sea water (2 : 1). The fixed nematodes were slowly transferred to pure glycerol and mounted in anhydrous glycerol or in Kaiser's glycerol gelatine (*en face* preparations).

Preparation for scanning electron microscopy (SEM). The same fixatives used for LM were used for the primary fixation of the living nematodes. Each specimen, still in fixative, was then temporarily transferred to a slide and covered by a cover glass supported by glass rods. The identification of species and the examination of sex and degree of maturity were performed by LM. After 1-3 days in the fixative, the specimens were washed in 0.2 mol/l cacodylate buffer and postfixed in 1 % osmium tetroxide in the same buffer for 1-2 h. at room temperature. After being washed in buffer, the specimens were dehydrated by passing them through a graded series of ethanol of increasing concentration to pure freon or by graded ethanol-acetone series, critical point-dried with CO_2 (COHEN, 1974), mounted on metal stubs, coated with gold in argon atmosphere, and examined in a Jeol JSM-U3 or a Jeol JSM-35 scanning electron microscope. The temporary study by LM before postfixation sometimes impaired the quality of the SEM preparations.

The number of specimens of each species and category (juveniles, females, males) studied by LM and SEM is given in Tab. 1. Only fully mature specimens are included in the categories « females » and « males ».

III. RESULTS

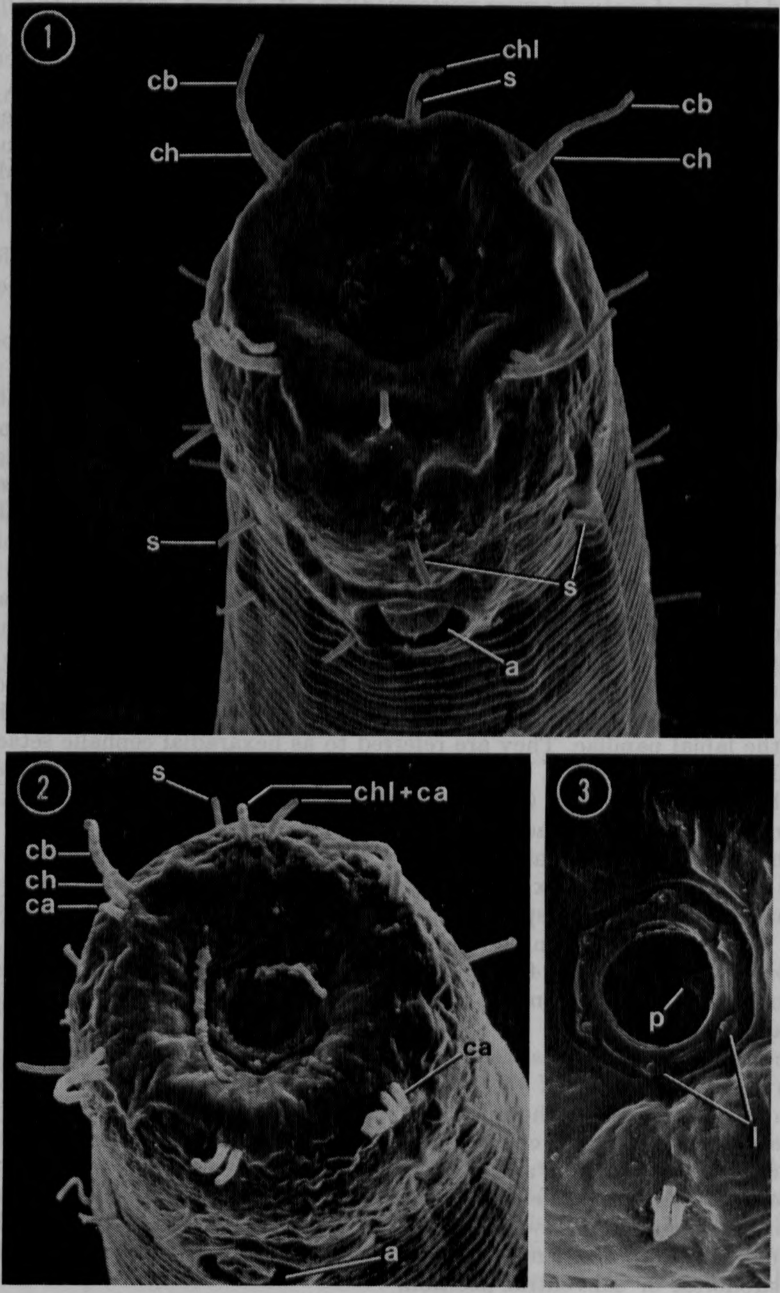
Within Linhomoeidae the arrangement of the cephalic sense organs (papillae, setae) is used to distinguish different genera (or groups of genera). A circle of six labial papillae and a circle of ten cephalic setae are reported to be characteristic of the genus *Paralinhomoeus* and some related genera. In the following this arrangement is called the basic pattern. Regular deviations from this pattern were observed in four of the five species studied.

The basic pattern is illustrated by the scanning electron micrograph of a *P. lepturus* female (Fig. 1). The circular mouth opening is surrounded by six minute lips, each bearing a small, labial papilla (cf. Fig. 3). The lips and their papillae are located in distinct positions, lateral, subdorsal, and subventral. The second circle of sense organs consists of ten cephalic setae. Six of them are short and located in the same radii as the labial papillae. They are referred to as hexaradial cephalic setae (*ch*, or in lateral position *chl*, in Fig. 1). The four longer setae (*cb*) of the cephalic setae are bilaterally arranged (cf. DE CONINCK, 1950). They are situated close to the subdorsal and subventral hexaradial setae. Four of the five species (exception : *P. ilenensis*) have subcephalic setae (*s* in Fig. 1) in distinct positions.

The basic pattern of six papillae and ten cephalic setae was observed in all young juveniles of the five species studied, and in the adults of *P. ilenensis* (*I* in Fig. 4). It was also found in the majority of the females of *P. lepturus* (*II*) and *P. intermedius* (*III* in Fig. 4). Of the five species studied, only *P. ilenensis* was found to have the same number of cephalic setae in juveniles, in adult females, and in adult males.

The males of *P. lepturus* were found to have 12-16 cephalic setae (Fig. 4). In addition to the ten setae of the basic pattern, two additional setae were always found in lateral positions. These two additional setae were observed already in old juveniles with distinct male characters. In adult males additional setae were found also near the short subdorsal and subventral hexaradial setae. However, the number of the latter additional setae varied from one to four. In Fig. 2 a male is shown with four additional setae ; two almost lateral, one almost subdorsal and one almost subventral. A few of the females studied were also found to have one additional seta in subdorsal or subventral position.

The males of *P. intermedius* were found to have six additional setae, one near each of the six short hexaradial cephalic setae. The four additional setae in almost subventral and subdorsal positions are easy to identify since they are somewhat shorter than the hexaradial ones (indicated in Fig. 4) and situated just outside the circle formed by the original cephalic setae.



Figs. 1-3. — Scanning electron micrographs of *Paralinhomoeus lepturus*. 1. Anterior end of a female (× 1800) ; 2. Anterior end of a male (× 1800) ; 3. Mouth opening and labial papillae (× 3000).

a = amphid, ca = additional cephalic seta, cb = bilateral cephalic seta, ch = hexaradial cephalic seta, chl = hexaradial cephalic seta in lateral position, l = labial papilla, p = tooth-like cuticular projection, s = subcephalic seta.

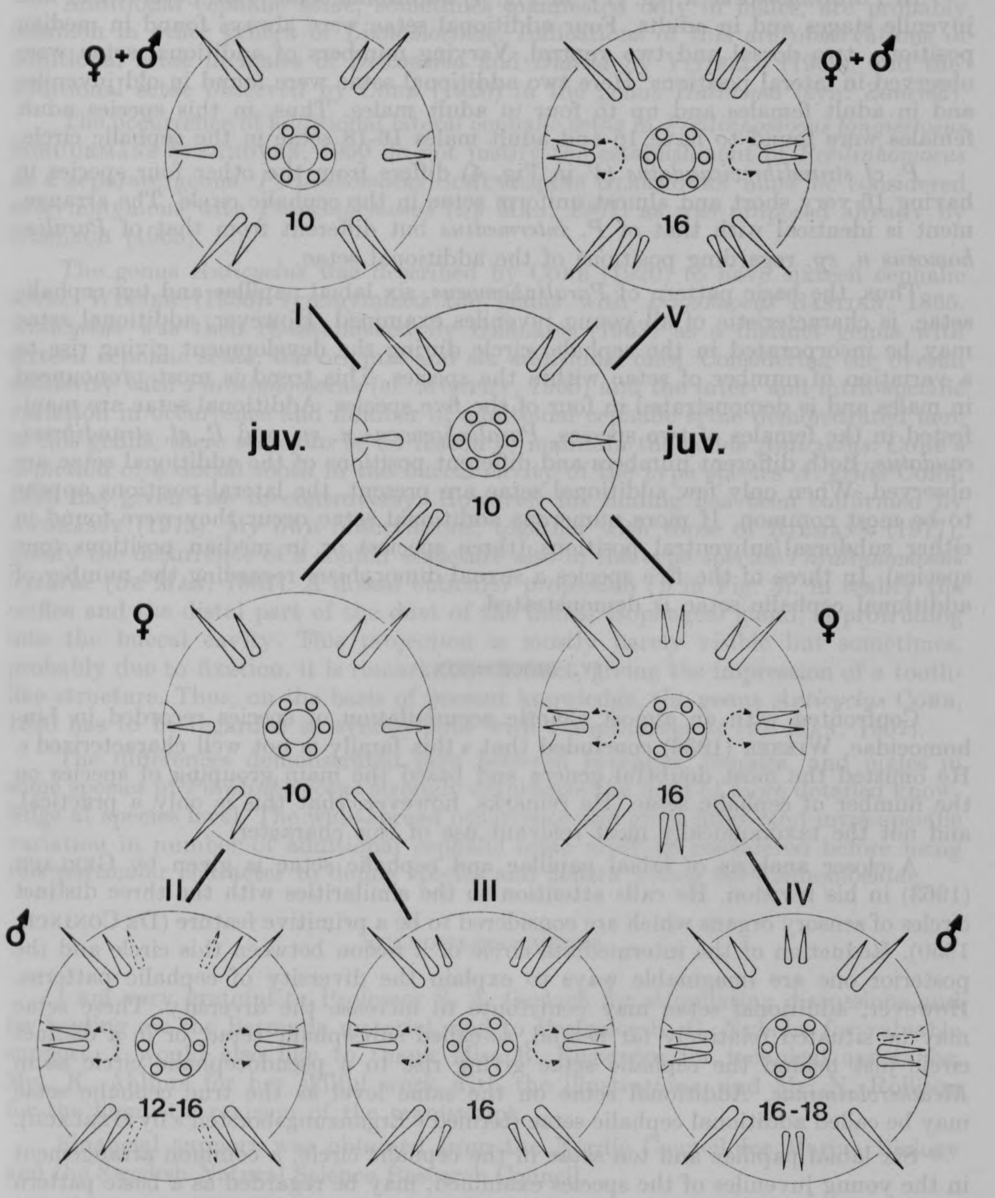


Fig. 4. — Schematic diagram illustrating the numbers and groups of cephalic setae in the five species :

I. *Paralinhomoeus ilenensis*
II. *P. lepturus*
III. *P. intermedius*
IV. *Paralinhomoeus n. sp.*
V. *P. cf strandibrevicaudatus.*

In *Paralinhomoeus n. sp.* (*IV* in Fig. 4) additional setae were observed in late juvenile stages and in adults. Four additional setae were always found in median positions, two dorsal and two ventral. Varying numbers of additional setae were observed in lateral positions. Here two additional setae were found in old juveniles and in adult females and up to four in adult males. Thus, in this species adult females were found to have 16 and adult males 16-18 setae in the cephalic circle.

P. cf strandibrevicaudatus (*V* in Fig. 4) differs from the other four species in having 16 very short and almost uniform setae in the cephalic circle. The arrangement is identical with that of *P. intermedius* but different from that of *Paralinhomoeus n. sp.* regarding positions of the additional setae.

Thus, the basic pattern of *Paralinhomoeus*, six labial papillae and ten cephalic setae, is characteristic of all young juveniles examined. However, additional setae may be incorporated in the cephalic circle during the development giving rise to a variation of number of setae within the species. This trend is most pronounced in males and is demonstrated in four of the five species. Additional setae are manifested in the females of two species, *Paralinhomoeus n. sp.* and *P. cf. strandibrevicaudatus*. Both different numbers and different positions of the additional setae are observed. When only few additional setae are present, the lateral positions appear to be most common. If more numerous additional setae occur they were found in either subdorsal/subventral positions (three species) or in median positions (one species). In three of the five species a sexual dimorphism regarding the number of additional cephalic setae is demonstrated.

IV. DISCUSSION

Confronted with an almost chaotic accumulation of species recorded in Linhomoeidae, WIESER (1956) concluded that « this family is not well characterized ». He omitted the most doubtful genera and based the main grouping of species on the number of cephalic setae. He remarks, however, that this is only a practical, and not the taxonomically most relevant use of this character.

A closer analysis of labial papillae and cephalic setae is given by GERLACH (1963) in his revision. He calls attention to the similarities with the three distinct circles of sensory organs which are considered to be a primitive feature (DE CONINCK, 1950). Reduction of the intermediate circle or a fusion between this circle and the posterior one are imaginable ways to explain the diversity of cephalic patterns. However, additional setae may contribute to increase the diversity. These setae may be situated relatively far behind, so-called subcephalic setae, or in a distinct circle just behind the cephalic setae giving rise to a pseudocephalic circle as in *Eleutherolaiminae*. Additional setae on the same level as the true cephalic setae may be called additional cephalic setae (termed « Ergänzungsborsten » by GERLACH).

Six labial papillae and ten setae in the cephalic circle, a common arrangement in the young juveniles of the species examined, may be regarded as a basic pattern in Linhomoeinae and very few exceptions are reported. However, occasional observations of additional cephalic setae have been reported earlier within *Paralinhomoeus*, by DE MAN (1907), SCHULZ (1932), and VITIELLO (1969). In some descriptions such setae have been depicted but not mentioned. Recently RIEMANN (1977) reported additional setae in lateral positions in a male of *P. lepturus*, and he also mentions the possibility of sexual dimorphism. These reports and the results obtained in the present study indicate that additional setae is a regularly occurring feature in many species of *Paralinhomoeus*.

Additional cephalic setae, sometimes manifested only in males, are probably common in other genera of *Linhomoeinae*. Indications of this are observations of additional setae in males of *Disconema* and *Didelta* by VITIELLO (1969), and the additional setae observed by COBB (1920) in the genus *Halinema* (syn. *Zanema*).

The occurrence of additional lateral cephalic setae in *Perilinhomoeus longisetosus* SCHUURMANS STEKHOVEN, 1950 do not justify the establishment of *Perilinhomoeus* as a separate genus. *Perilinhomoeus* SCHUURMANS STEKHOVEN must be considered as synonymous with *Paralinhomoeus* (DE MAN, 1907) as was proposed already by GERLACH (1963).

The genus *Anticyclus* was described by COBB (1920) to have sixteen cephalic setae. WIESER (1956) synonymized the genus with *Linhomoeus* BASTIAN, 1865. *Anticyclus* was then re-established by GERLACH (1963) as a distinct genus with sixteen cephalic setae, ten original and six additional ones. Considering the overall similarity with *Paralinhomoeus* (cf. MURPHY, 1965) and the inter- and intra-specific variation in occurrence and number of additional cephalic setae demonstrated here in this genus, there seems to be no reason to maintain the genus *Anticyclus*. COBB's depiction of a dorsal tooth in the buccal cavity of the type species *A. exilis* COBB, 1920 has given rise to controversy. However, his finding has been confirmed by ANDRÁSSY (1973). My own observations, together with those of RIEMANN (1977), justify the occurrence of a similar structure also in the type species *Paralinhomoeus lepturus* (DE MAN, 1907). A dorsal cuticular projection (*p* in Fig. 3), in reality the orifice and the distal part of the duct of the dorsal esophageal gland, is protruding into the buccal cavity. This projection is mostly barely visible but sometimes, probably due to fixation, it is remarkably distinct, giving the impression of a tooth-like structure. Thus, on the basis of present knowledge, the genus *Anticyclus* COBB, 1920 has to be regarded as synonymous with *Paralinhomoeus* (DE MAN, 1907).

The differences demonstrated here between juveniles, females, and males in some species of *Paralinhomoeus* strongly emphasize the need of more detailed knowledge at species level. The wide-spread occurrence and great inter- and intra-specific variation in number of additional cephalic setae must be considered before using this particular character to define species and genera within the Linhomoeidae.

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SUPERFAMILY CERAMONEMATOIDEA (COBB, 1933) GENERAL MORPHOLOGY

by

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ABSTRACT

The systematics of the superfamily Ceramonematoidea is mainly based on morphological characteristics. A detailed study is made of the most important structures : the general shape, the cuticle and the epidermis, the musculature, the cephalic region, the digestive, nervous, excretory and reproductive systems, and the juvenile stages.

In a previous paper (HASPESLAGH, 1972) some evolutionary trends of the Ceramonematoidea have been shown, and a revision of the systematics has been proposed. The present paper brings a more detailed study of some morphological structures.

GENERAL SHAPE

The body length of adults in the different species of the different families is comprised between ± 400 µm and 2500 µm, without appreciable differences in males and females.

In cylindriform animals the body diameter remains nearly constant all over the body (Pl. I, fig. 1), while in oblong spindleshaped animals it is attenuated in the cephalic and the tail region (HASPESLAGH, 1972, Pl. I, fig. 7) ; generally females are less slender than males, the body diameter being influenced by the development of the oöcytes.

Short specimens often are fixed in a stretched position, while long specimens often curl up. In most males the tail is bent or curved ventrally, always to the right (Pl. I, fig. 1).

Several genera have a distinct annulated outlook due to the very coarse cuticular annules (Pl. I, fig. 1).

CUTICLE

The cuticular structure and its growing complexity is one of the most important morphological characteristics of the group.

The cuticle is always well developed : without the crests the cuticular layers easily take up 1/4-1/5 of the body diameter (Pl. II, fig. 6).

A distinct annulation is due to regular transverse constrictions in the superficial and median cuticular layers.

In *Xenella cephalata* COBB, 1920 the annule width of the ± 2000 annuli reaches only 0.5 μm, but in most species the number of annuli is reduced while their width varies between 5 and 12 μm.

The annule width remains constant all over the body, or varies in different ways as described in HASPESLAGH 1972, p. 238-239 (Pl. I, figs. 4 and 7).

In the anal region often two annuli partially or completely fuse into a clearly broader annulus ; in a *Pselionema* spec. a similar phenomenon has been noticed in the vulvar region.

As far as we could examine the number of annuli on the tail remains constant in juveniles and in adults of the same species, and the excretory pore is situated in the same annulus in juveniles and in adults. So the increase of the total number of annuli in the successive stages is due to an increase of the annuli in mid-body ; in some species growing zones can be distinguished, e.g. in *Cyttaronema* spec. in the region behind the cardia (Pl. I, fig. 5) and in the preanal region, where often duplicating annuli are present.

The long terminal annulus is probably formed by the fusion of several tail annuli ; in some species this process is still visible in adults (Pl. I, fig. 8).

Besides a distinct annulation the cuticle of Ceramonematoidea is characterized by longitudinal crests all over the body, but interrupted between the consecutive annuli. The crests on the annuli have a simple structure, or consist of a rather strong base surmounted by a very thin epicrista (Pl. II, fig. 6 and HASPESLAGH, 1972, fig. 1). Sometimes the crests include small spheric structures, with a refraction-index (or a density) different from that of the surrounding cuticular materials (Pl. I, fig. 7).

Together with the tendency of increasing in width, the structure of the cuticular annuli becomes more complex (HASPESLAGH, 1972, p. 236 and fig. 1).

The median layer of the cuticle has a homogeneous structure (Pl. I, fig. 7), or contains inclusions of a different density and of various shapes. These so-called vacuoles are spread all over the annulus (Pl. I, fig. 5), or are restricted to the area under the longitudinal crests (Pl. I, fig. 4).

PLATE I

Fig. 1 — *Ceramonema* spec., ♂ : cylindriform shape, coarse cuticular annules, tail bent to the right ;

Fig. 2 — *Pselionema rigidum* CHITWOOD, 1936, ♀ : longitudinal fibers in the cuticle and cells of the epidermis ;

Fig. 3 — *Cyttaronema* spec., ♂ : copulatory muscles in the tail ;

Fig. 4 — *Ceramonemoides chitwoodi* (DE CONINCK, 1942) HASPESLAGH, 1972, ♀ : cuticle at vulvar level ;

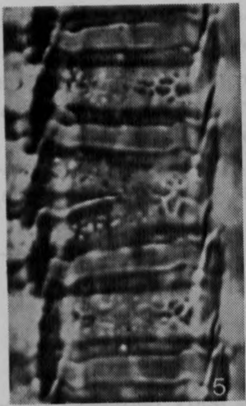
Fig. 5 — *Cyttaronema* spec. : duplicating annulus in the postcephalic region ;

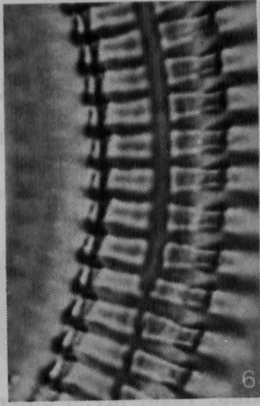
Fig. 6 — *Leptodasynemella albaensis* (WARWICK and PLATT, 1973), ♀ : lateral « field » ;

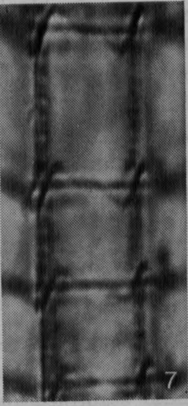
Fig. 7 — *Pselionema simile* DE CONINCK, 1942, ♂ : broad/narrow annules, light refracting elements in the longitudinal crests ;

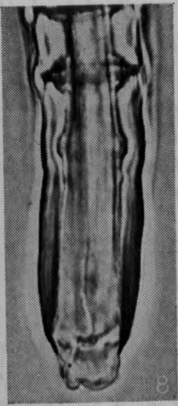
Fig. 8 — *Ceramonema attenuatum* COBB, 1920, ♀ : terminal annulus with indication of inclusion of an annule, and obtuse mucron with separate outlet of the three caudal glands.

PLATE I









In or near the basal layer sometimes longitudinal fibers are visible in the middle of the annular fields ; they probably contribute in keeping together the consecutive annuli (Pl. I, fig. 2).

In a few species the reinforced parts of the median layer are partly interrupted in the annules along the « lateral fields » of the postcephalic region (Pl. I, fig. 6).

On the tail of most males there are two rows of setae in subventral or lateroventral position ; exceptionally the tail of some females too bears some small dispersed setae.

EPIDERMIS

Large cells have regularly been observed in the lateral epidermis (Pl. I, fig. 2), and often groups of 3-4 small cells with a very large nucleus at regular intervals in the dorsal and ventral chord.

In numerous species very small pores occur all over the body except on the tail, situated in four sublateral rows although sometimes widely dispersed. These pores probably are in connection with epidermal gland cells through the cuticle, but it is not excluded that they perform also sensory functions.

Each of the three caudal glandcells probably has a separate outlet through the mucron of the terminal annulus (Pl. I, fig. 8).

MUSCULATURE

Because of the presence of a very thick cuticle the longitudinal muscles of the body wall can not clearly be distinguished.

In the anterior part of the tail of many males copulatory muscles have been observed (Pl. I, fig. 3). The cells are situated on both sides and have a broad laterodorsal anterior insertion on one tail annulus, an oblique course, and a narrow subventral posterior insertion on the second next tail annulus. These muscle cells are responsible for the ventral bend or curving of the tail.

CEPHALIC REGION

The presence of a distinct head- or cephalic capsule at the very anterior end of the body is one of the important characteristics of the Ceramonematoidea.

The shape of the capsule is rather variable : open in front (Pl. II, fig. 5) or enclosing the labial region (Pl. II, figs. 1 and 2) ; short- or elongated cylindrical (Pl. II, fig. 2), conical (Haspeslagh 1972, Pl. II, fig. 2) or of a transitional form ; the anterior part is rounded (Pl. II, fig. 2) or flattened (Pl. II, fig. 5), or has a transitional form, it sometimes is less cuticularized than the basal part of the capsule,

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PLATE II

Fig. 1 — *Cyttaronema* spec. ♀ : cephalic region ;

Fig. 2 — *Pselionema* spec. ♂ : cephalic region ;

Fig. 3 — *Dasynemella sexalineatum* Cobb, 1920, juv. : anterior body end with oesophagus (after Cobb) ;

Fig. 4 — *Cyttaronema* spec. : « en face » view ;

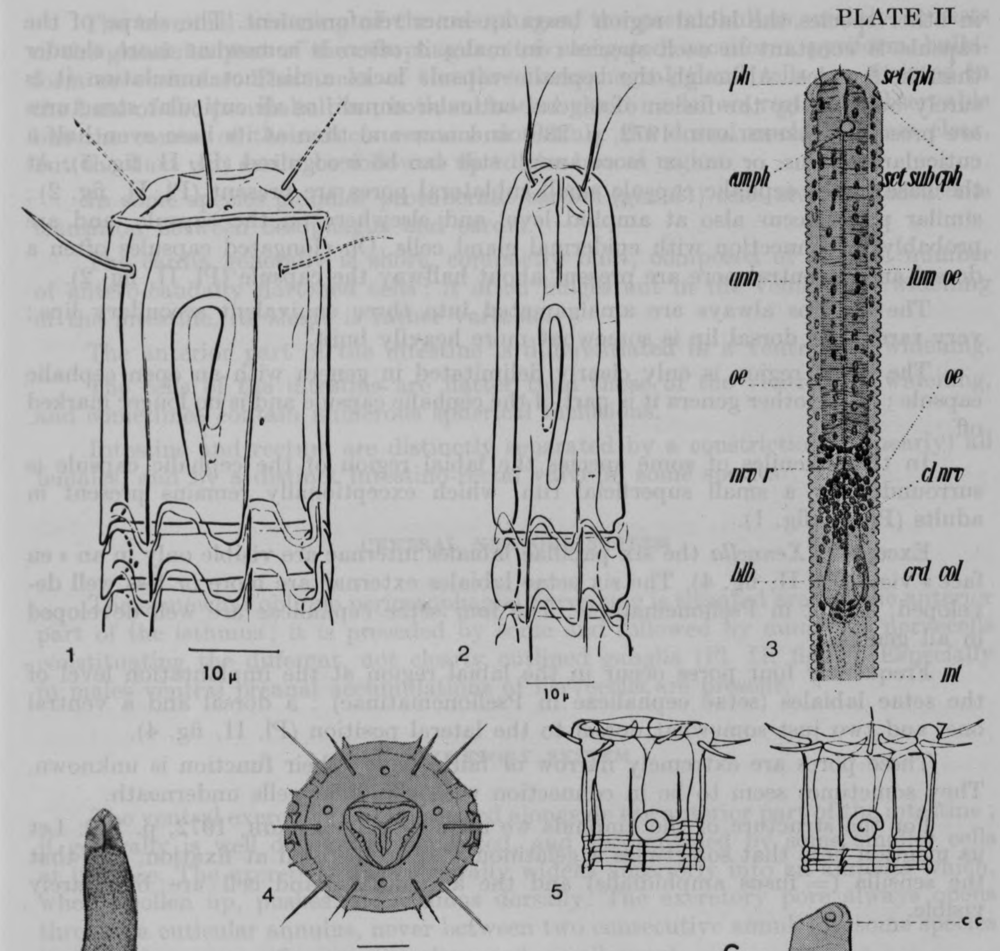
Fig. 5 — *Metadasynemoides latus* (Gerlach, 1957) Haspeslagh, 1972 : cephalic region ♀ and ♂ (after Gerlach) ;

Fig. 6 — *Cyttaronema* spec. : cuticular annule in front view ;

Fig. 7 — *Cyttaronema* spec., ♀ : gonads ;

Fig. 8 — *Cyttaronema* spec., fourth juvenile stage ♀ : genital primordium, cc : capcell, gc : germinative cell with large nucleus, sc : epithelial cell, vk : nucleus in the ventral chord.

PLATE II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in other species the labial region bears an inner reinforcement. The shape of the capsule is constant in each species ; in males it often is somewhat more slender than in females. Although the cephalic capsule lacks a distinct annulation it is surely built up by the fusion of several cuticular annuli, as all cuticular structures are present (HASPESLAGH, 1972, p. 239) and now and then at its base even half a cuticular annulus, or one or more annuli still can be recognized (Pl. II, fig. 5). At the base of the cephalic capsule small sublateral pores are present (Pl. II, fig. 2) ; similar pores occur also at amphid level and elsewhere on the capsule, and are probably in connection with epidermal gland cells. On elongated capsules often a dorsal and a ventral pore are present about halfway the capsule (Pl. II, fig. 2).

The six lips always are amalgamated into three equivalent secondary lips ; very rarely the dorsal lip is somewhat more heavily built.

The labial region is only clearly delimitated in genera with an open cephalic capsule ; in the other genera it is part of the cephalic capsule and is no longer marked off.

In the juveniles of some species the labial region of the cephalic capsule is surrounded by a small superficial rim, which exceptionally remains present in adults (Pl. II, fig. 1).

Except in *Xennella* the six papillae labiales internae are visible only in an « en face » view (Pl. II, fig. 4). The six setae labiales externae are more or less well developed, except in Pselionematinae. The four setae cephalicae are well developed in all genera.

Frequently four pores occur in the labial region at the implantation level of the setae labiales (setae cephalicae in Pselionematinae) : a dorsal and a ventral one, and two just somewhat dorsal to the lateral position (Pl. II, fig. 4).

These pores are extremely narrow or fairly wide ; their function is unknown. They sometimes seem to be in connection with glandular cells underneath.

For the structure of the amphids we refer to HASPESLAGH, 1972, p. 240. Let us mention here that sometimes a gelatinous bar is liberated at fixation, and that the sensilla (= fusus amphidialis) and the amphidial gland cell are but rarely visible.

DIGESTIVE SYSTEM

There is no distinct buccal cavity, and except for teethlike cheilorhabdia in some species there are no distinct cuticularisations.

The oesophagus consist of a corpus, an isthmus and a terminal pseudobulbus (Pl. II, fig. 3). At its most anterior part it is suspended by a cephalic septum to the cuticularized base of the lips and to the body wall. The cylindrical, muscular corpus makes out the main part of the oesophagus. All over its length the muscle fibers mainly have a radial position, only in the labial region there is a short, more or less distinct differentiation (Pl. II, fig. 2). The inner wall of the corpus is sometimes interrupted, but these minute interruptions are not always in accordance with muscular zones.

The delimitation between corpus and isthmus is usually clear. The isthmus is shorter, and weakly or hardly muscular. Its anterior part is surrounded by the nerve ring. The excretory ampulla lays also at isthmus level, and its condition highly determines the shape of the isthmus and even of the pseudobulbus.

The terminal widening of the oesophagus, the pseudobulbus, mainly consists of the glandular part of the oesophagus ; it is elongated, sacciform, pyriform, bulbiform or vesicular. The nuclei of the three oesophageal gland cells are situated in the base of the pseudobulbus ; both sublateral gland nuclei are regularly observable but the course of their ducts remains doubtful ; the dorsal nucleus is less clear, but the duct can easily be followed up to the buccal region.

In some species globular protuberant cardial (gland?) cells are situated at the transition between oesophagus and cardia.

The cardia generally is short, compactly built, composed of a small number of antero-caudally flattened cells ; it often bulges out in the ventricular widening of the intestine, its shape is rather variable.

The anterior part of the intestine is differentiated in a ventricular widening.

The cells of the intestine are flatter than those of the ventricular widening, and sometimes contain numerous spherical inclusions.

Intestine and rectum are distinctly separated by a constriction in (nearly) all females, and by a distinct intestino-rectal valve in some species.

CENTRAL NERVOUS SYSTEM

The somewhat oblique perioesophagial nerve ring is situated around the anterior part of the isthmus ; it is preceded by some and followed by numerous nervecells constituating the different, not clearly outlined ganglia (Pl. II, fig. 3). Especially in males ventral preanal accumulations of nervecells are present.

EXCRETORY SYSTEM

The ventral excretory cell is situated alongside the anterior part of the intestine ; it generally is well developed, elongated, and accompanied by some smaller cells at its base. The excretory duct generally widens anteriorly into an ampulla which, when swollen up, pushes the isthmus dorsally. The excretory pore always opens through a cuticular annulus, never between two consecutive annuli ; in some species it opens by means of a narrow, elongated, small spout.

REPRODUCTIVE SYSTEM

Females (Pl. II, fig. 7)

Gonads opposite, equivalent and reflexed, generally situated alternatively to one and to the other side of the intestine.

The germinative zone is short and rounded, often pressed against the spermatheca. In the growth zone very few oöcytes develop at once, in most species only one alternating in the anterior and the posterior gonad, stretching the wrinkled epithelium. A fullgrown oöcyte is very large : a length of 180 μm has been noticed ; a large growing oöcyte often pushes the corresponding germinative zone towards and even beyond the vulvar level.

The oviduct is thinwalled.

The spermatheca is thinwalled, often bulging from the uterus and separated from the rest of the uterus by a sphincter.

The shell gland (= tricolumella, quadricolumella, crustaformeria) often has large swollen cells, even when no oöcytes are ripening in the corresponding gonad. A fertilized egg is thinwalled and stretches the uterus. Each uterus is in connection with the vagina.

The vagina is generally surrounded by a strong sphincter ; sometimes vaginal glands are present near the uterine wall.

The vulva consist of a transverse slit, situated between two consecutive annuli ; only in one *Pselionema* spec. the vulva is situated in the middle of a large, double vulvar annulus. In *Pselionema rigidum* CHITWOOD, 1936 an egg with a developing embryo was still attached to the vulva by eggmembranes. There is a cuticular reinforcement around the vulvar slit ; it is limited to both the vulvar annuli in species with broad cuticular annuli, but in species with narrow annuli, several annuli partly fuse together and build up a broad lipstructure. In *Metadasynemella macrophalla* DE CONINCK, 1942 a vulvar apron (epiptygma) is constituted, probably by concrescence of zygapophysae.

Males (Pl. III)

Two testes, opposite and stretched, the posterior is always less developed than the anterior.

The germinative zone is short and is immediately followed by a zone of differentiation. Immediately after formation spermatozoa often lay piled up in the form of a stack, but further they lay more disorderly.

The wall of the gonoduct often is granular (possibly indicating a glandular function), the granules are smaller than the nuclei of spermatids or spermatozoa. Often there is a short, fine dotted zone at about the junction of both gonoducts, where the vas deferens starts.

The wall of the vas deferens contains many gland cells all over its length, having a different outlook (different function?) in the consecutive zones. Three (very) coarsely granulated glandcells (= ejaculatory glands?) situated in the distal part of the vas deferens in the cloacal region often grow out far anteriorly, sometimes nearly reaching the testes.

The spicula are equal in length, more or less ventrally bent ; the capitulum is more or less cylindrical, the calamus (corpus) is chiefly cuticularized ventrally and dorsally, the distal part of the lamina has also lateral cuticularisations. The spicula of the different species and genera all are built on the same pattern, and seldom show good specific characteristics.

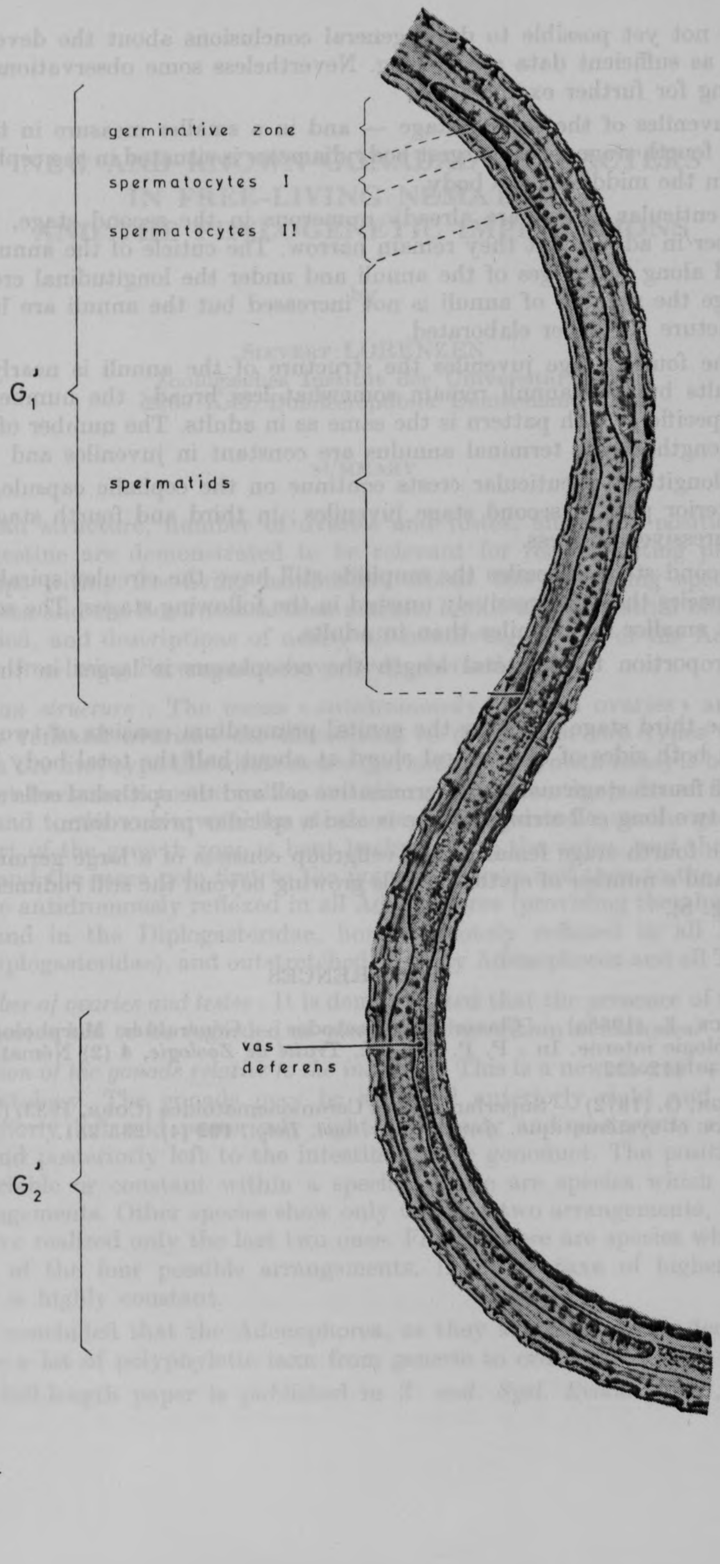
The gubernaculum generally is about half as long as the spicula. It consists of a single or double, heavily cuticularized median piece, and two rather long lateral pieces (wings), which distally form the gliding grooves for the spicula.

In most species the protractor of the gubernaculum is well developed ; the whole copulatory musculature is only exceptionally to be observed.

PLATE III

Cyttaronema spec., ♂ : gonads.

PLATE III


germinative zone
spermatocytes I
spermatocytes II
G₁
spermatids
vas deferens
G₂

JUVENILE STAGES

It is not yet possible to draw general conclusions about the development in juveniles as sufficient data are lacking. Nevertheless some observations are worth mentioning for further examination.

In juveniles of the second stage — and in a smaller measure in those of the third and fourth stage — the largest body diameter is situated in the cephalic region, and not in the middle of the body.

The cuticular annuli are already numerous in the second stage, 60-80 % of the number in adults, but they remain narrow. The cuticle of the annuli is mostly developed along the ridges of the annuli and under the longitudinal crests. In the third stage the number of annuli is not increased but the annuli are broader and their structure is further elaborated.

In the fourth stage juveniles the structure of the annuli is nearly the same as in adults but the annuli remain somewhat less broad ; the number of annuli and the specific growth pattern is the same as in adults. The number of tail annuli and the length of the terminal annulus are constant in juveniles and adults.

The longitudinal cuticular crests continue on the cephalic capsule, nearly up to its anterior part in second stage juveniles ; in third and fourth stage juveniles they progressively regress.

In second stage juveniles the amphids still have the circular spiral structure ; in most species they progressively unwind in the following stages. The setae remain somewhat smaller in juveniles than in adults.

In proportion to the total length the oesophagus is larger in the youngest stages.

In the third stage juveniles the genital primordium consists of two small cell-groups on both sides of the ventral chord at about half the total body length.

In the fourth stage males the germinative cell and the epithelial cells are dividing and form two long cell strings ; there is also a spicular primordium.

In the fourth stage females each cellgroup consists of a large germinative cell, a capcell and a number of epithelial cells growing beyond the still rudimental vagina (Pl. II, fig. 8).

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NEW AND KNOWN GONADAL CHARACTERS IN FREE-LIVING NEMATODES AND THE PHYLOGENETIC IMPLICATIONS

by

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SUMMARY

Ovarian structure, number of ovaries and testes, and their position relative to the intestine are demonstrated to be relevant for reconstructing phylogenetic relationships within free-living nematodes. About 600 free-living species of the Adenophorea and the Secernentea from marine, limnic and terrestrial biotopes have been studied, and descriptions of nearly all free-living species of the Adenophorea and many free-living Secernentea have been checked.

Ovarian structure : The terms « antidromously reflexed ovaries » and « homodromously reflexed ovaries » are introduced to distinguish two types of reflexed ovaries. In the first type the whole ovary (germinal and growth zone) is bent against the oviduct backwards to the vulva, and the ova move to the point of flexure with one pole and to the vulva with the other one. In the second type the germinal and only a part of the growth zone is bent backwards to the vulva, and the ova move with one and the same pole first to the point of flexure and then to the vulva. The ovaries are antidromously reflexed in all Adenophorea (providing they have reflexed ovaries) and in the Diplogasteridae, homodromously reflexed in all Rhabditida (except Diplogasteridae), and outstretched in many Adenophorea and all Tylenchida.

Number of ovaries and testes : It is demonstrated that the presence of two ovaries and two testes has to be regarded as plesiomorphic within nematodes.

Position of the gonads relative to the intestine : This is a new character introduced into nematology. The gonads may be arranged anteriorly right and posteriorly left, anteriorly left and posteriorly right, anteriorly and posteriorly right or anteriorly and posteriorly left to the intestine or the gonoduct. The position may be either variable or constant within a species. There are species which display all four arrangements. Other species show only the first two arrangements, while again others have realized only the last two ones. Finally there are species which display only one of the four possible arrangements. In many taxa of higher rank this character is highly constant.

It is concluded that the Adenophorea, as they are presently understood, contain quite a lot of polyphyletic taxa from generic to order rank.

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ULTRASTRUCTURE OF THE CUTICLE OF *SABATIERIA* (NEMATODA, CHROMADORIDA) AND ITS PHYLOGENETIC SIGNIFICANCE

by

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ABSTRACT

The ultrastructure of the cuticle of *Sabatieria pulchra* was studied. It consists of a thick cortical layer with striated appearance, an electron translucent median layer traversed by very dense rods and a basal layer consisting of two fibrous sublayers. The structure of the cuticle does not provide a definite hint concerning the systematic position of the Comesomatidae.

INTRODUCTION

The Comesomatidae with their very abundant genus *Sabatieria* ROUVILLE, 1903 have a somewhat questionable systematic position. In the presently accepted system they are placed among the Chromadorida but there are arguments against such position (structure of ovaries, oesophagus, excretory organ : see RIEMANN, 1977). Because of the doubtful status of the systematic position of the Comesomatidae an investigation on the ultrastructure of the cuticle of *Sabatieria* has been conducted.

MATERIAL AND METHODS

The material originated from the Weser Estuary. Small body sections were fixed in cold 2,5 % glutaraldehyde solution (buffered at pH 7,4) for 2 hours, then washed and postfixed in 1 % osmium tetroxide for 2 hours. For better handling the pieces were embedded in agar then dehydrated in ascending grades of ethanol, treated with propylene oxide and embedded in Araldit. Sections were stained with uranyl acetate and lead citrate. They were studied in an EM-9 Zeiss electron microscope.

OBSERVATIONS

The cuticle of *Sabatieria pulchra* (G. SCHNEIDER, 1906) has a very complicated ultrastructure (Figs. 1a, b). The basal layer (labelled 3a, 3b) is divided into two well distinguishable sublayers. The inner part consists of a thick layer of crossed fibers which are arranged in several sublayers, comparable to the lamellar zone of *Xiphinema* (Dorylaimida) as described by ROGGEN et al. (1967). The fibers which make up the character of this zone are extremely strong and ribbonlike. They form an angle of about 90 degrees with each other (Fig. 1a).

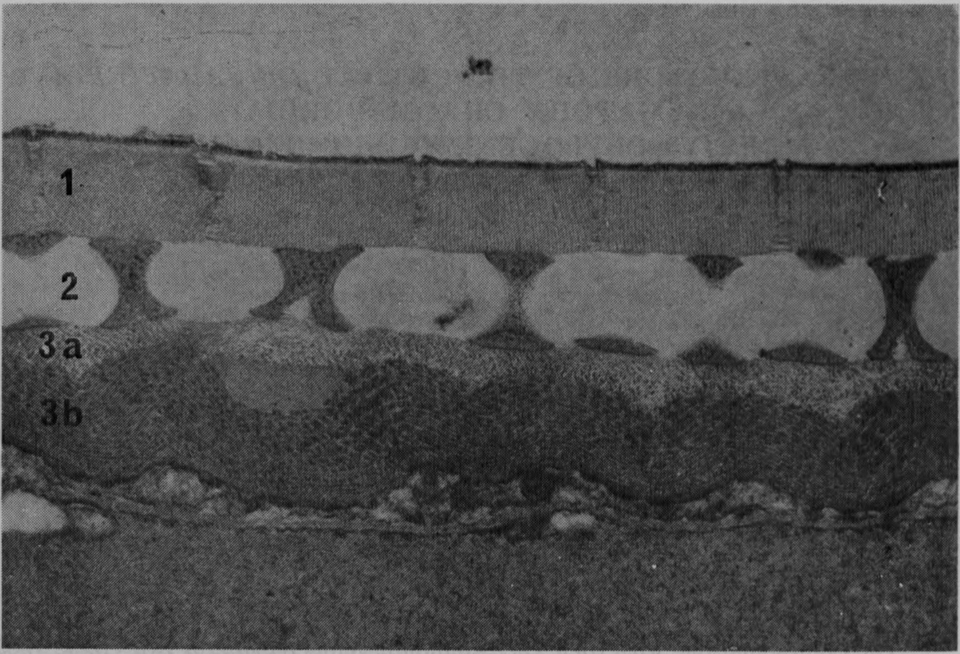

Fig. 1a. — Cross section of the cuticle of *Sabatieria pulchra* : 1) cortical layer, 2) median layer, 3a) outer part of the basal layer, 3b) inner part of the basal layer.

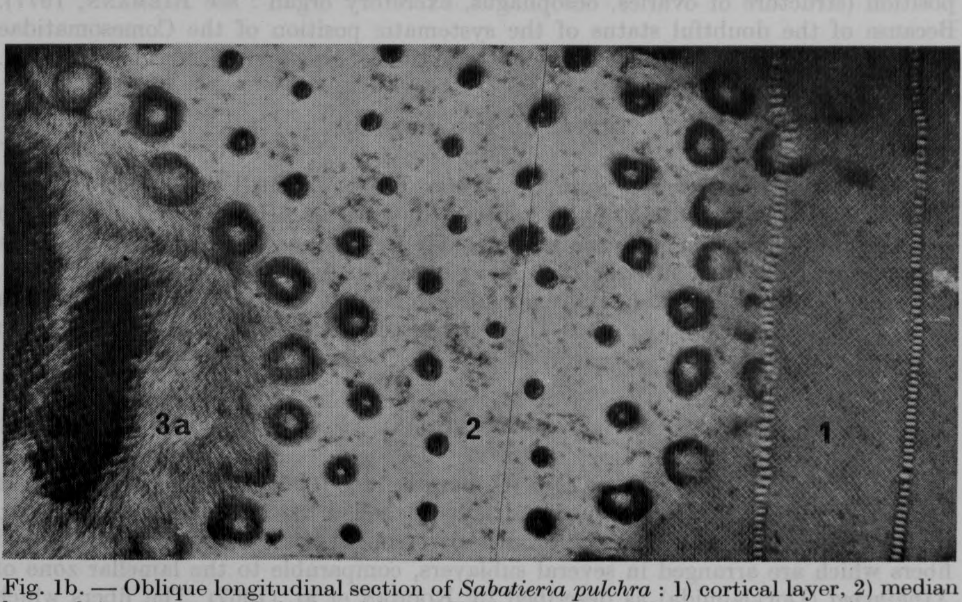

Fig. 1b. — Oblique longitudinal section of *Sabatieria pulchra* : 1) cortical layer, 2) median layer, 3a) outer part of the basal layer, 3b) inner part of the basal layer.

This zone is followed by a second one which in cross sections appears to consist of irregularly arranged fibers ; however, in oblique longitudinal sections it is obvious that these fibers are following a main direction and are arranged in two zones forming an angle of about 50 degrees with each other.

The median layer appears as an electron translucent zone traversed by extremely dense rods which are partially hollow. The rodlike arrangement of this dense material produces in the light microscope the image of cuticular punctation.

The median layer is covered by a thick cortical layer. In cross sections (Fig. 1b) this layer has a striated appearance, but in oblique longitudinal sections it is evident that this appearance is caused by parallel rows of rodlike structures crossing each other at right angles.

DISCUSSION

Asking now for the phylogenetic significance of the cuticle structure of *Sabatieria* there are certain similarities to Cyatholaimidae like *Acanthonchus* (Wright and Hope 1968). In both genera the cortical layer shows a striate appearance and the median layer appears as an electron translucent matrix traversed by electron dense rods. However, the basal layer in *Acanthonchus* is a very thin one while in *Sabatieria* it is very broad and divided into two sublayers which in their turn are subdivided. The rods which exist in the median layer of *Sabatieria* cannot be regarded to be characteristic for Chromadorida because such rodlike structures are also to be seen in the cuticle of the Rhabditida *Caenorhabditis* (Zuckerman et al., 1973) and *Eudiplogaster* (own observation on *Eudiplogaster pararmatus* (W. Schneider, 1938)] and even in the cuticle of Tardigrades as the recent work of Greven (1975) on *Halechiniscus* demonstrates.

On the other hand there are also similarities to *Xiphinema*. The second layer of this species possibly is not so structureless as it appears in cross sections ; the filaments observed by Roggen et al. (1967) may point to an indistinct striation of this layer which should be seen in oblique sections. In addition, the basal layer of *Xiphinema* has the same lamellar differentiation as the inner basal zone of *Sabatieria*. The total basal layer of *Sabatieria* is a very extended fiber layer. Such distinct crossed fiber layers are unknown as yet in the order Chromadorida but are occurring in Enoplida and Secernentea, as for example the cuticle of *Caenorhabditis* shows. Concluding, I would say that the cuticle of *Sabatieria* provides no definite hints which suggest that Comesomatidae should have a position within the Chromadorida.

ACKNOWLEDGEMENT

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ANATOMIC, HISTOLOGIC AND CYTOLOGIC STUDIES OF MEMBERS OF THE ORDER CHROMADORIDA

by

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SUMMARY

In 91 species belonging to the nematode order Chromadorida the anatomic, histologic and cytologic organisation of the functional systems (body wall, digestive tract, nervous system, reproductive systems) are analysed.

The Chromadorid cuticle is three-layered. The middle layer (matrix) is a hollow space, containing a skeleton, which causes the punctuation-pattern. Three main types of skeleton are discerned, and a survey of the structural variations is given. In the Chromadoridae the matrical organisation of the juvenile cuticle is uniform, but usually a more elaborate type of skeleton is formed during the last moult. Analysis of the punctuation-patterns in adult Chromadoridae revealed, that the different types are structurally only gradually different. A functional analysis of the cuticular architecture is given, in which a relation with the muscle structure is pointed out. A hypothesis concerning the hypermorphosis of the cuticle in the Chromadoridae is brought forward.

The epidermis contains epithelial cells and two types of gland cells, the secretory cycles of which are described at the ultrastructural level. These glands are associated with neural elements. The caudal glands and the ventral gland are specialised sub-epithelial glands of the same type. The cytological features and the secretory mechanism are identical. The ventral gland is accompanied by coelomocytes, which are thought to function in the elimination of substances from the pseudocoelom.

Comparative morphology of the stoma revealed a structural uniformity, except for the Comesomatidae. The stomatal apparatus consists of two functional systems : a dilatation mechanism of the cheilostoma and an operating mechanism of the dentition. The dilatation mechanism depends on the hydrostatic properties of a labial ventricle and the transformation of longitudinally directed into radial forces, in which the rugae play an important role. The muscular systems are divided in an intra- and an extra-oesophageal group. In *Chromadora nudicapitata* the intra-oesophageal group consists of direct and indirect tooth muscles, which open the oesophagostoma and erect the teeth. The extra-oesophageal muscles comprises 4 sets of muscles (protractors, retractors, indirect dilatatores buccae and a sphincter).

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In the stomatal armature two types of teeth are discerned. The concept onchium is redefined as a cuticularisation, which is incorporated into the stomatal wall during the moult following its formation. The nature of the stomatal dentition is analysed in the different subfamilies of the order.

The cellular organisation of the oesophagus of *C. nudicapitata* is reconstructed by serial sections at the ultrastructural level. 17 muscle cells, 51 marginal cells, 8 neurocytes, 5 gland cells and 2 cells of unknown nature have been located. Comparative morphology indicates, that the bulbar anatomy in the Chromadoridae is invariant, the structural differences being insignificant and of secundary origin.

The intestinal cells are characterised and their possible functions discussed. The structure of the rectum is described. In the Choniolaimidae and the Selachinematidae the rectum is not functional.

The nervous system of *C. nudicapitata* is reconstructed at the ultrastructural level. 72 ganglion cells have been identified. They form the circum-oesophageal ganglia (frontal, lateral and posterior ganglia), the postoesophageal ganglia and the peri-anal ganglia (preanal and lumbar ganglia). In addition, 20-30 isolated bipolar neurocytes are present in the epidermis. The cephalic nerves comprise 8 intraepithelial nerve trunks (median, lateral and submedian) and 4 submedian nerve trunks in the pseudocoelom. The ramifications and the commissures of these trunks are given in detail. The nervous system of the midbody is located in the epidermis (median, lateral and submedian). There are 6 caudal nerve trunks (median, lateral and laterodorsal). The histology of receptor-organs is described in detail (labial papillae, cephalic setae, amphid, amphidule, body pores, somatic setae, ocelli). Neurosecretory activity is detected in about 20 ganglion cells, the significance of which is discussed.

Comparative study of the female reproductive system showes a common basic anatomy (ovary, oviduct, compartimented uterus, cuticularised vagina) with structural variation in the histology of the oviduct, the compartimentation of the uterus, the structure and composition of the spiral valves and the presence of three different types of glands. In the male reproductive system the variation occurs in the number of testes, the structure of the full-grown vesicula seminalis, the presence of an uterus masculinus, the structure of the valves, the number of ejaculatory glands and the structure of the copulatory apparatus. The main characters of the spicular sclerotisations are depicted, which are related to the structure of the spicular musculature. The histology of the vas deferens is highly variable ; it is assumed, that the variations are related to the development and productivity of the testes.

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THE FUNCTION OF THE DEMANIAN SYSTEM AND AN ATYPICAL COPULATORY BEHAVIOUR IN *ONCHOLAIMUS OXYURIS*

by

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ABSTRACT

In this paper information concerning the function of the demanian system is presented and related to the atypical copulatory behaviour observed in *Oncholaimus oxyuris*. It appears that the system in this species at least is the usual site from which sperms enter the female reproductive system.

OBSERVATIONS

Oncholaimus oxyuris Ditlevsen, 1911 was maintained in agar cultures at room temperature and observations were made on living specimens in observation chambers as described by Maertens (1976). Formalin fixed and glycerin mounted specimens were used for more detailed morphological observations.

The demanian system of *O. oxyuris* is typical of the genus (cf. Rachor, 1969) and consists of a very long and narrow ductus uterinus (about 10-14 body-widths long), a well developed uvette, and a rather wide main duct leading posteriorly to several terminal ducts which end in pores, and anteriorly to a ductus entericus connected with the intestine through a rather poorly defined osmosium. The ductus entericus is slightly longer than the main duct. The terminal pores are usually preanal or adanal in position and are variable in number (Fig. 1) ; sometimes a secretion may adhere to the pores.

In agar cultures copulation was only occasionally observed ; it continued for up to 20 min. The frequency of mating can be considerably increased by storing the cultures for at least three days in the dark at 10° C and subsequently transferring them to daylight at room temperature, after which most of the mature specimens copulate within 24 h. Mature females always had some oocytes within the gonoduct. Males touching the posterior end of such females react violently and bring their tail end in contact with that of the female. Insemination is usually effected by the introduction of the spicules into one of the preanal terminal pores of the female's demanian system. During mating the partners may form an acute or obtuse angle with eachother (Fig. 2), or may be orientated in opposite directions. After ejaculation sperm cells are quickly shifted to the main duct where they cluster behind a dark plug of secretory material. The spermatozoa then pass through the uvette into the ductus uterinus and from there to the uterus, where the oocytes are fertilised. A few hours later the eggs become surrounded by an egg shell. The

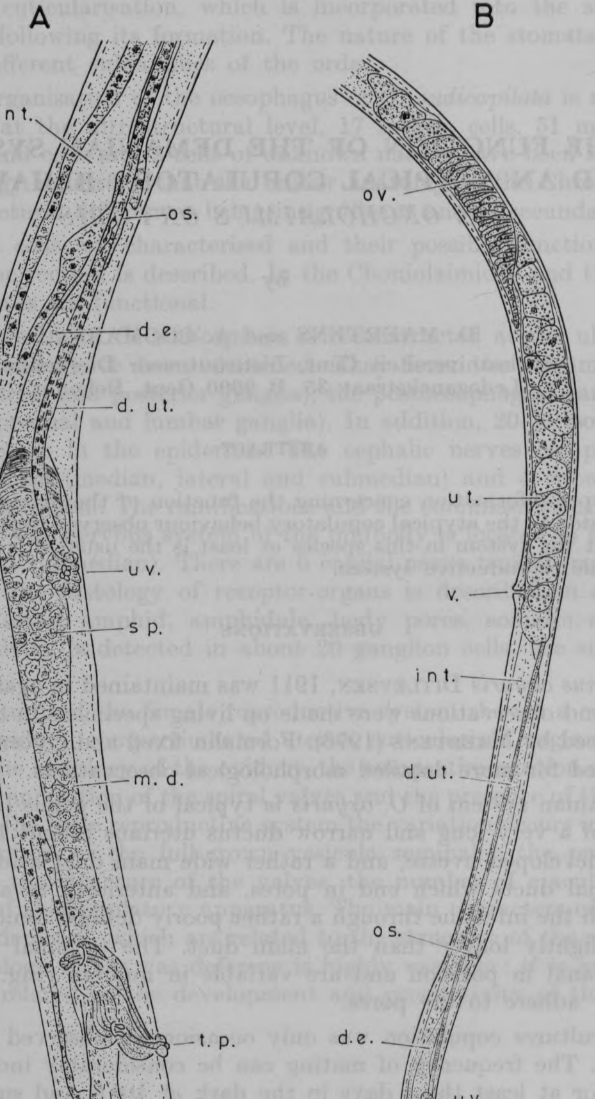

Fig. 1. — *Oncholaimus oxyuris* A : posterior part of the demanian system after copulation ; B : female reproductive system.

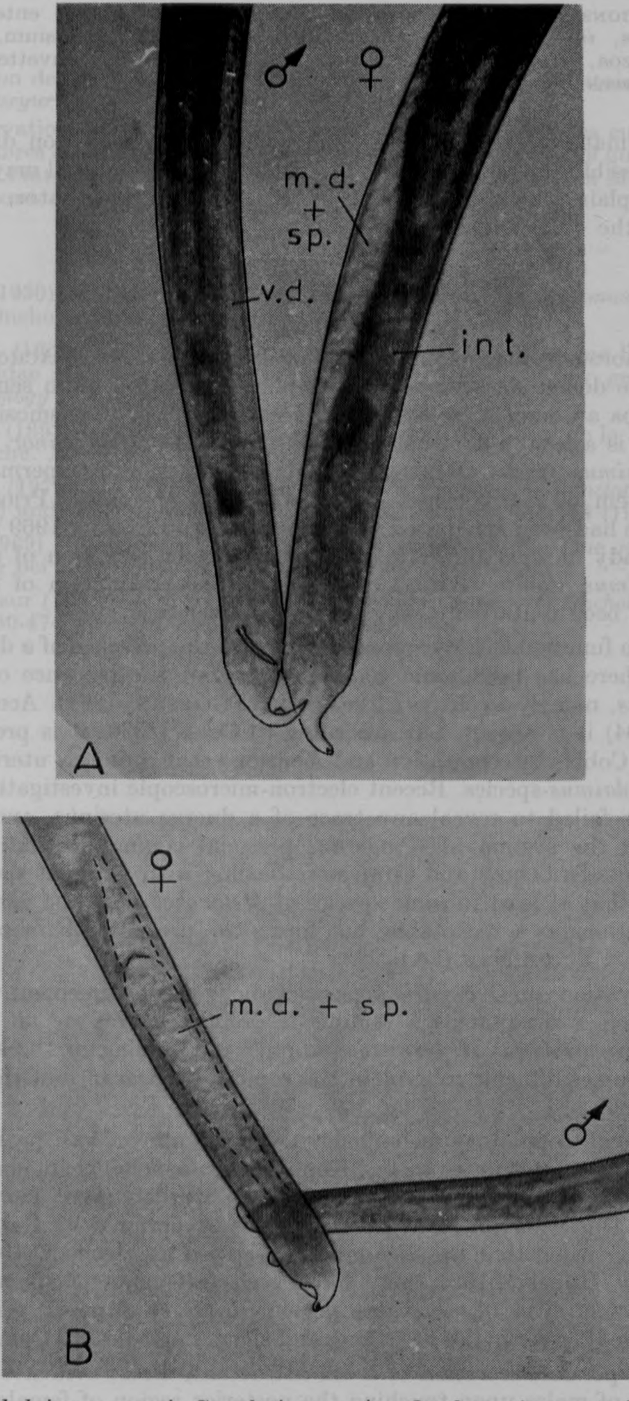

Fig. 2. — *Oncholaimus oxyuris* Copulation — A : fixed specimens (spicules retracted during fixation) ; B : living specimens.

ABBRÉVIATIONS : *a.* = anus, *cop.* = copulation, *d.e.* = ductus entericus, *d.ut.* = ductus uterinus, *int.* = intestine, *m.d.* = main duct, *os.* = osmosium, *ov.* = ovary, *sp.* = spermatozoa, *t.p.* = terminal pore, *ut.* = uterus, *uv.* = uvette, *v.* = vulva, *v.d.* = vas deferens.

remaining spermatozoa, together with the plug of secretion, soon disappear from the system. Possibly they disintegrate, and the remaining material may be absorbed. This would explain why only one day after copulation, spermatozoa are difficult to observe in the demanian system.

DISCUSSION

After a thorough and comparative morphological study, RACHOR (1969) concluded that the demanian system is a complicated receptaculum seminis in which the spermatozoa are kept alive by help of secretions from the osmosium. Although good evidence is available for some species such as *Meyersia minor* HOPPER, 1967 and *Adoncholaimus fuscus* (BASTIAN, 1865), the presence of spermatozoa in the demanian system of many other species was only presumed. Prior to RACHOR, other functions had been attributed to the system (see RACHOR, 1969 for a complete review) : Already in 1893 DE MAN had postulated the secretion of a preanal belt in *Metoncholaimus albidus* (BASTIAN, 1865) and the production of a kind of sex attractant has been tentatively suggested several times.

In order to function as a receptaculum seminis the presence of a ductus uterinus is essential. There has been some controversy about the presence of this duct in *Metoncholaimus*, namely in *M. pristiurus* (ZUR STRASSEN, 1894). According to ZUR STRASSEN (1894) it is absent, but according to COBB (1930) it is present. RACHOR (l.c.) accepted Cobb's interpretation and mentions that a ductus uterinus is present in all *Metoncholaimus*-species. Recent electron-microscopic investigation of *M. pristiurus* however failed to reveal any trace of a ductus uterinus, and sperms were not present in the system (J. CALCOEN, personal communication). Hence, it is possible that ZUR STRASSEN and COBB were dealing with different species. Furthermore it seems that at least in some species of *Metoncholaimus* the demanian system no longer functions as a receptable, but forms the preanal belt of mature females as first observed by DE MAN (l.c.).

The observations on *O. oxyuris* presented above are in agreement with RACHOR's conclusion when a receptaculum seminis is defined merely as an organ for the reception of spermatozoa. If, however, storage and feeding of the spermatozoa is implied, it becomes difficult to explain the rapid disappearance of the spermatozoa from the system.

The atypical copulatory behaviour described above was probably seen by VON THUN, but was interpreted as « ... Kopulationsversuche, bei denen die Spicula... durch die Kutikula des Hinterkörpers gestossen wurde » (VON THUN in RACHOR, 1969, p. 152). This behaviour was believed to be exceptional by RACHOR (l.c.) who nevertheless suggested that the « scytalia » described by HOPPER (1967) for *Metoncholaimus pelor* HOPPER, 1967, may have been fragments of spicules broken off during copulation. The observations presented above support this assumption, especially since *M. pelor* males have long and slender spicules that may easily break.

As to the possible secretion of a sex attractant, direct evidence is lacking but the behaviour of males upon touching the posterior region of females is suggestive of such a secretion.

RÉSUMÉ

La fonction de l'organe de de Man et un comportement copulatoire atypique chez *Oncholaimus oxyuris*.

Des observations sur des individus vivants, maintenus dans des cultures d'agar et dans des chambres d'observation, et sur des spécimens fixés ont relevé que l'insemination est réalisé par l'intermédiaire des pores terminaux de l'organe de de Man. La fonction de cet organe est discutée.

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SPECULATIONS ON THE PRIMITIVE NEMATODE AND THE EARLY EVOLUTION OF THE CLASS NEMATODA

by

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SUMMARY

For the reconstruction of the phylogeny the discrimination of primitive and derived characters is indispensable. This can be done by using the criteria of (1) systematic character precedence, (2) geological character precedence, (3) chorological criteria, (4) criterion of ontogenetic character precedence, (5) teratological criterion, (6) functional criteria. The value of these criteria for recognizing the primitive nematode is discussed and with particular consideration of functional aspects (turgor pressure hypothesis) the arguments favouring the assumption of the primitivity of the Trichodoroidea, Diphtherophoroidea, Onchulinae and Tripyla are presented. Regarding the oldest bifurcation steps in the evolution of nematodes the Adenophorea/Secernentea and the Enoplia/Chromadoria concept is critically examined. It is suggested to consider the marginal oesophageal tubes as an early derived character shared by Monhysteridae, Araeolaimida, Comesomatidae and Secernentea thus indicating the monophyletic origin of these taxa.

THE EXCRETION ORGAN OF *SABATIERIA* (NEMATODA, CHROMADORIDA) AND ITS PHYLOGENETIC SIGNIFICANCE

by

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SUMMARY

Sabatieria (Comesomatidae) has not only an uninucleated ventral gland cell as other Chromadorida but in addition lateral ducts are attached to the excretory ampulla. The lateral ducts are ending in pyriform uninucleated glands laying far behind the oesophageal region. This situation reminds of a secernentean type of excretory organs.

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THE TAXONOMIC REQUIREMENTS OF ECOLOGISTS

by

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SUMMARY

Of the two branches of taxonomy, *systematics* (classification and phylogeny) is considered by most practitioners to be the most innovative and challenging, whereas the provision of an *identification* service for other biologists is considered as a secondary chore. Although the principal topic of this meeting is systematics, I hope that we will be able to devote some attention to the way this second responsibility can be met, because after all it is only systematists that can meet it.

Most ecologists will admit the ecological importance of nematodes but their role is difficult to evaluate unless the species can be separated : they occupy a large number of niches in the food web and cannot be lumped together in studies of ecological processes. In the currently fashionable study of diversity, species must also be identified and, in applied fields such as pollution studies, it is often possible to recognise species which are indicators of particular ecological conditions. However, ecologists have historically been daunted by the excessive number of species which may be present in any one sample, by the probability that a proportion of the taxa will be undescribed, and by the lack of comprehensive keys and handbooks, or of specialists with enough time to devote to their samples.

The provision of centres to which the ecologist can send his samples for identification is not a satisfactory solution to the problem in the long term. We must therefore ensure that the present state of knowledge is distilled into a form which can be used by the non-specialist in the form of keys and handbooks. The production of popular syntheses of this kind is by no means a simple task — it can be every bit as challenging as primary systematic studies and far more time-consuming. However, the advantages would far outweigh the effort. So what is the best way to go about it? Is it premature to produce handbooks for certain geographic regions when it is clear that there are many species still to be found? Should we use dichotomous or tabular keys? Are keys or lists of species on a habitat basis a practical proposition? I hope that this paper will promote discussion on these and other questions : as the prospective co-author of such a handbook, I would welcome advice !

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FREELIVING MARINE NEMATODES OF ANTARCTICA
A CURRENT APPRAISAL

by

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ABSTRACT

Early studies of marine nematodes from Antarctic waters, based on collections made by various national expeditions between 1882 and 1931, were primarily descriptive in nature and specimens were often poorly preserved and unrepresentative of the total fauna. Emanating from broader-based approaches to problems of life in low-temperature environments, new and more comprehensive collections have recently been made. In the Atlantic sector of the Antarctic Ocean, material from shallow sublittoral areas in South Georgia and the west coast of the Antarctic Peninsula have been obtained by diving and by grab-sampling in deeper waters off South Georgia and in the Weddell Sea. The new material should enable some of the earlier descriptions to be improved in addition to providing new information. It is suggested that detailed studies of nematode communities could provide a valuable method of addressing some of the classical aspects of Antarctic biology.

INTRODUCTION

The Antarctic Ocean is one of the richest biological provinces on earth. Man's current interest in its resources is directed primarily towards exploiting the krill and fish stocks. As coastal regions, particularly around South Georgia, are of prime importance to the breeding and early development of certain commercially important species, near-shore benthic ecosystems are currently the subject of investigation by the British Antarctic Survey.

Much recent work has addressed fundamental ecological and physiological problems of life in these low-temperature environments. With increasing awareness of the possible importance of nematodes, the group has been included in some of these investigations.

This submission gives a brief review of past and current interest in Antarctic marine nematology and describes the scope and progress of the British Antarctic Survey's work in the field.

GENERAL REVIEW

The marine Antarctic region, for the purposes of this review, is considered to

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be that area south of the Antarctic Convergence (Fig. 1). But because of their proximity to the Convergence and the present lack of agreement on the limits of various biogeographical areas (HEDGPETH, 1970), the sub-Antarctic Kerguelen and Macquarie Islands have been included.

Scientific publications concerned with Antarctic nematodes are few. The first nematode to be described from Antarctic waters was *Deontostoma antarcticum* (v. LINSTOW, 1892) collected at South Georgia during the German International Polar-Year Expedition (1882-1883). Subsequently, less than thirty taxonomic papers have been published, recording about 500 species (~ 70 % new) : most describe animals collected by various national expeditions (Table 1). Unfortunately, many are descriptions of poorly preserved specimens, often unrepresentative of the populations from which they came.

About half the publications are those of ALLGÉN. Initially, he described 13 nematodes collected by Larsen's Ross Sea Expedition (1929-1930) at Macquarie Island and in the Ross Sea (ALLGÉN, 1929-1930). Later, he worked with collections made in South America, the Falkland Islands, South Georgia and the Antarctic Peninsula by Nordenskjold's Swedish Antarctic Expedition (1901-1903), recording almost 400 species of which about 60 % were new (ALLGÉN 1952-1960). Many new species descriptions were of single female or juvenile specimens and the figures, particularly in the two major works (ALLGÉN, 1959, 1960), are rather inadequate. Other reports of nematodes from the Atlantic sector were from the South Orkneys by VON LINSTOW (1907a), from South Georgia by STEINER (1921) and from the Antarctic peninsula by INGLIS (1958).

VON LINSTOW (1907b) also provided the first description of a nematode from the East Antarctic (*Leptosomatum australe* from the Ross Sea). Later, COBB (1914) described 25 new species collected in the Ross Sea by Shackleton's expedition (1907-1909). Epsilonematidae and Desmoscolecida, collected by the German Antarctic Expedition (1901-1903), were described by STEINER (1931a, 1931b) and TIMM (1970) respectively. MAWSON's two Antarctic expeditions (1911-1914, 1929-1931) provided material which resulted in the valuable contributions of COBB (1930) and MAWSON (1956-1958b). Further descriptions of Enoplida from Kerguelen Island were made by SCHUURMANS STEKHOVEN and MAWSON (1955) and PLATONOVA (1958). Other early papers, dealing with non-taxonomic aspects of Antarctic nematology, were given by ALLGÉN (1934, 1952b, 1952d, 1953c, 1955) and COBB (1916).

In recent times, the establishment of permanent biological facilities in the Antarctic, such as those at Kerguelen Island, Palmer Station, Signy Island and South Georgia, have enabled more detailed long-term biological investigations to be undertaken. The results are only slowly becoming available, but studies involving nematodes have been reported from the Ross Sea (HOPE, 1974 ; TIMM and VIGLIERCHIO, 1970) and Kerguelen Island (ARNAUD, 1974 ; DE BOVÉE, 1975 ; DE BOVÉE and SOYER, 1975), in addition to the work to be described here.

PRESENT INVESTIGATION

Two approaches were adopted. Firstly, a wide ranging series of collections around the Scotia Arc and in the Weddell Sea were made, specifically for nematological purposes. Secondly, a more detailed year-round population study was undertaken at South Georgia. The former was intended to satisfy some basic questions of geographical variation and species diversity. The latter had a more ecological basis, but should also enable infra-specific variation in cold waters to be investigated.

TABLE 1

Antarctic expeditions providing samples from which free-living marine nematodes have been described

Dates	Name of Expedition	Leader	Vessel	Principal collection areas	Principal publications
1882-1883	German International Polar-Year Expedition	Neumayer	Germania	South Georgia	v. Linstow, 1892
1901-1903	Swedish Antarctic Expedition	Nordenskyöld	Antarctic	South Georgia, Antarctic Peninsula	Allgén, 1952-1960
1901-1903	German Antarctic Expedition	Drygalski	Gauss	Kerguelen Island, Wilkes Land	Steiner, 1931a, 1931b ; Timm, 1970
1901-1904	National Antarctic Expedition (British)	Scott	Discovery	Ross Sea	v. Linstow, 1907b
1902-1904	Scottish National Antarctic Expedition	Bruce	Scotia	South Orkney Islands	v. Linstow, 1907a
1907-1909	National Antarctic Expedition (British)	Shackleton	Nimrod	Ross Sea	Cobb, 1914
1910-1912	British Antarctic Expedition	Scott	Terra Nova	Ross Sea	Leiper & Atkinson, 1915
1911-1914	Australasian Antarctic Expedition	Mawson	Aurora	Macquarie Is, Wilkes Land	Cobb, 1930 ; Mawson, 1958a, 1958b
1923-1924	Ross Sea Expedition (Norway)	Larsen	Sir James Clark Ross	Ross Sea, Macquarie Island	Allgén, 1929-1930
1929-1931	British-Australian-New Zealand Expedition	Mawson	Discovery	Various east Antarctic areas	Mawson, 1956, 1958a, 1958b

TABLE 2

Main sampling locations

Location	Bearings	Water depth (m)	Sampling method (*)
Stanley Harbour, Falkland Islands	51°41′S, 57°40′W	2-5	D
King Edward Cove, South Georgia	54°17′S, 36°30′W	5-20	D
« Offshore », South Georgia	53-56°S, 35-37°W	108-282	G
Maxwell Bay, South Shetland Islands	62°12′S, 58°56′W	6	D
Deception Island, South Shetland Islands	62°59′S, 60°34′W	17	D
Kristi Cove, Anvers Island	64°47′S, 64°03′W	20	D
Grotto Island, Argentine Islands	65°14′S, 64°16′W	10	D
Avian Island, Adelaide Island	67°46′S, 68°54′W	18	D
Back Bay, Stonnington Island	68°12′S, 67°0′ W	15	D
Mobster Creek, Halley Bay	75°31′S, 26°42′W	220	G

(*) D = diving, G = grab.

Biogeographical Study. The main sampling locations are detailed in Table 2 and shown in Figs. 1 and 2. Whenever possible, material was obtained quantitatively by SCUBA diving, using hand-held cores. Samples from the Falkland Islands and the Antarctic Peninsula were obtained in March/April 1974 operating from the R.R.S. Bransfield. In February, 1975, a series of Smith-McIntyre grab samples were taken from a depth of 220 m off the Brunt Ice Shelf near Halley Bay. Although the main South Georgia programme was located in King Edward Cove, several samples were obtained from other areas. These included a series of offshore grab samples kindly supplied by the staff of the Polish research vessel Professor Siedlecki in February, 1976. The locations were similar to those of the Swedish Antarctic Expedition quoted by ALLGÉN (1959). From these various South Georgia collections, it is hoped to be able to improve some of the original taxonomic descriptions.

Temporal Population Study. The long-term study was based on a shallow (4-6 m) fine sand area during 1975 and 1976. The annual range of various environmental factors (e.g. water temperature — 0.2° to + 3.8°; salinity 31.4 ‰ to 34.1 ‰) describe the general stability of the habitat. Of those parameters monitored, only pigment values varied significantly, being higher during the austral summer (average sediment chlorophyll *a* values from November to March, 15.5 μg/g and from April to October, 3.9 μg/g). Preliminary data indicated nematode densities within the range generally expected for the substrate type (580 ± 90 ind./cm^2), and an assemblage superficially resembling that normally expected from comparable habitats in European waters. However, the main part of the faunal analysis remains to be completed.

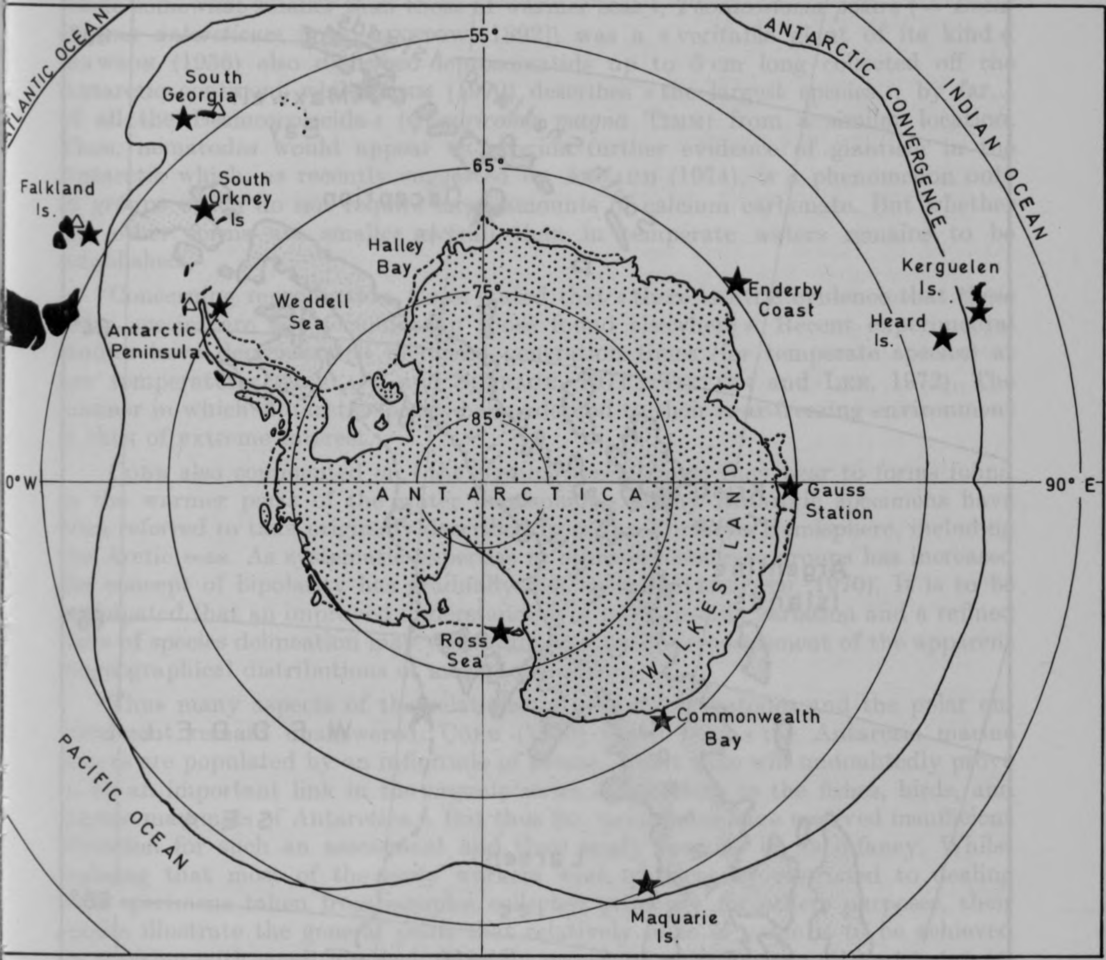

Fig. 1. — Map of Antarctica and the Southern Ocean indicating principal collecting sites of (✱) extant publications on Antarctic nematodes and (△) this study.

DISCUSSION

The Antarctic marine environment is characterised by near-constant low temperatures but great seasonal variations in primary productivity (EL-SAYED, 1970 ; EVERSON, 1977). Initial studies of Antarctic benthos, mainly of epifaunal communities, led to suggestions of metabolic cold adaptation, reproductive adaptation, slow growth, low species diversity, high biomass, giantism (much larger size than similar species in other seas) and bipolar species distributions (ARNAUD, 1974 ; EVERSON, 1977 ; KNOX, 1970). In addition, attempts were made to delineate major biogeographic regions. Controversy still surrounds many of these concepts, partly because of what DUNBAR (1970) referred to as the « taxonomic jungle of the higher latitudes » and partly as more information concerning the infauna becomes available.

Fig. 2. — Map of Antarctic Peninsula showing (★) main diving locations detailed in Table 2.

The intrinsic advantages of marine nematode populations, namely high densities and species diversity, enable them to be sampled quantitatively with relatively little logistic effort. Thus, they should provide an ideal means of studying some of these classical problems of biology in a polar context.

As long ago as 1914, Cobb made several salient points regarding Antarctic nematodes. On their size, he observed that although « antarctic species are on the whole somewhat smaller than those of warmer seas », *Thoracostoma polare* (= *Deontostoma antarcticum* [VON LINSTOW, 1892]) was a « veritable giant of its kind ». MAWSON (1956) also described leptosomatids up to 5 cm long collected off the Antarctic continent while TIMM (1970) describes « the largest species... by far... of all the Desmoscolecida » (*Quadricoma magna* TIMM) from a similar location. Thus, nematodes would appear to provide further evidence of giantism in the Antarctic which, as recently suggested by ARNAUD (1974), is a phenomenon only in groups which do not require large amounts of calcium carbonate. But whether the other forms are smaller overall than in temperate waters remains to be established.

Concerning reproduction, COBB stated that « there is little evidence that these polar species are less fecund than those found elsewhere ». Recent experimental studies have demonstrated increased generation times (for temperate species) at low temperatures (GERLACH and SCHRAGE, 1971 ; TIETJEN and LEE, 1972). The manner in which Antarctic species have adapted to their near-freezing environment is thus of extreme interest.

COBB also commented on « the striking resemblance they bear to forms found in the warmer parts of the water hemisphere ». Many Antarctic specimens have been referred to taxa originally described from the Northern Hemisphere, including the Arctic seas. As systematic expertise in other invertebrate groups has increased the concept of bipolarity has gradually lost favour (HEDGPETH, 1970). It is to be anticipated that an improved understanding of infra-specific variation and a refined basis of species delineation may well result in a similar reassessment of the apparent biogeographical distributions of marine nematodes.

Thus many aspects of the relationship between nematodes and the polar environment remain unanswered. COBB (1930) noted that « the Antarctic marine waters are populated by an infinitude of nemas... that time will undoubtedly prove to be an important link in the organic series culminating in the fishes, birds, and marine mammals of Antarctica ». But thus far, nematodes have received insufficient attention for such an assessment and their study remains in its infancy. Whilst realising that most of the early workers were of necessity restricted to dealing with specimens taken from samples collected primarily for others purposes, their results illustrate the general point that relatively little of value is to be achieved by working with small numbers of badly preserved or unrepresentative specimens. With the comparative scarcity of marine nematode expertise, it cannot be recommended too strongly that where opportunities for study occur, more effort should be directed towards meaningful objectives, wherever possible linked to the work of ecologists.

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INVESTIGATIONS ON NEMATODES IN THE EMS-DOLLART ESTUARY

by

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SUMMARY

Heavy pollution of the canals in the Dutch province of Groningen with effluent from many potato flour-mills and straw board factories causes much irritating stink. This obliged the government to consider other means of getting rid of the effluent. Being less expensive than clearance of the effluent, the construction of a pipeline from the industrial area to the Ems-Dollart estuary was proposed to solve this problem. Lack of knowledge about the biological effects of an increased discharge of organic waste materials directly into the estuary, forced the government to initiate the formation of a research group : « Biological Research Ems-Dollart Estuary » (BOEDE). The research team includes microbiologists, phycologists and zoologists and is supposed to describe relevant biological processes in the estuary and to predict possible shifts in the ecosystem caused by changing the discharge of effluent. Meiofauna is one of the subjects investigated. Research started with a survey of nematodes in the area between the island of Borkum and Nieuwe Statenzijl.

This paper describes observations on nematode populations in the area that is influenced directly by the effluent. The area is situated in the south-east of the Dollart, near the waste water outlet at Nieuwe Statenzijl, and consists of tidal mudflats. The sediment is silty, very rich in organic matter and covered with a film of brown coloured diatoms. Regularly anaerobic water masses pass by. The black sulfide layer is located near the sediment surface at a depth of three mm. The extremely thin oxidized sediment layer is mainly colonized by bacteria, nematodes and oligochaetes. This region lacks macrofauna, while meiofaunal organisms such as copepods, which are abundant in other parts of the estuary, disappear during the flourmill campaign. From this thin zone of oxidized sediment nematodes have been isolated and identified throughout a year ; 100 to 200 nematodes were identified eight times. The isolations included seven to ten different species which is a very low number compared with samples from other parts of the estuary. Distribution of specimens over the species was very uneven. Dominances of 40 to 95 % have been found of the following species : *Eudiplogaster pararmatus*, *Hypodontolaimus geophilus*, *Theristus setosus* and *Anoplostoma viviparum*. A special survey of this area was carried out to detect if pollution effected the meiofauna. From September on the discharge of effluent increases because the factories start processing the new potato harvest. Six sediment samples were taken at distances of 500 m among themselves, on a line from Nieuwe Statenzijl to Emden. The first sampling

station was located at a distance of one km from the effluent outlet into the Dollart, the sixth station two and a half km farther in the direction of Emden (Fig. 1).

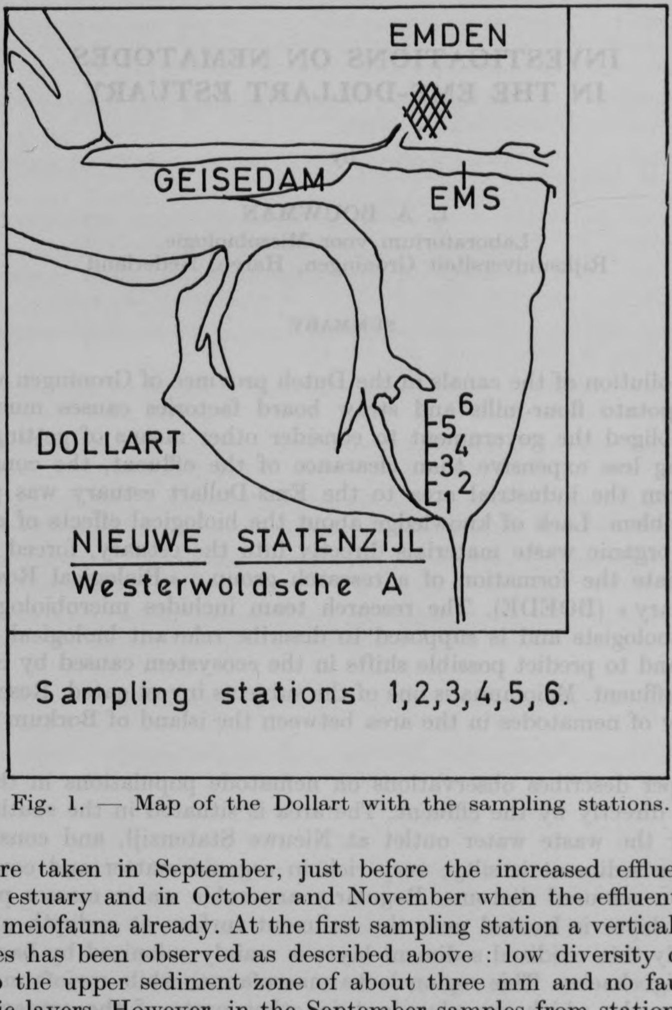

Fig. 1. — Map of the Dollart with the sampling stations.

Samples were taken in September, just before the increased effluent discharge reached the estuary and in October and November when the effluent could have effected the meiofauna already. At the first sampling station a vertical distribution of nematodes has been observed as described above : low diversity communities, restricted to the upper sediment zone of about three mm and no fauna at all in the anaerobic layers. However, in the September samples from station two, a zone below the superficial sediment has been recognized which is colonized mainly with the nematode species *Sabatieria vulgaris*. At the other stations the same phenomenon has been observed. The dominant colonisation by this species of the zones just below the superficial sediment has been noticed in all muddy areas of the estuary. In October and November, during the flourmill campaign, the species *Sabatieria vulgaris* practically disappeared from the stations two and three respectively, while at the other stations the numbers of specimens did not fluctuate very much (Table 1). It seems that the species investigated prefers semi-aerobic conditions, available in the layer below the upper three mm of the sediment in muddy areas. These conditions shift from semi-aerobic to anaerobic during the flourmill campaign at the stations two and three ; consequently the species *Sabatieria vulgaris* disappears.

TABLE 1

Sabatieria vulgaris *specimens/cm*^{3}

Station number	1	2	3	4	5	6
September	2	115	69	56	72	80
October	4	18	44	65	95	86
November	0	10	3	96	80	—

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THE ECOPHYSIOLOGY OF MARINE NEMATODES

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SUMMARY

The ecophysiology of any group of animals is best approached by analysing the responses of organisms to individual environmental factors as well as to combinations of factors. Very little has been done along these lines in marine nematodes and very few findings of a more general nature have emerged. The following topics of recent interest should be mentioned, however :

1) *Temperature*

Resistance studies revealed relationships between upper lethal temperature and the patterns of distribution in various species. A closer analysis of this relationship may prove fruitful in shedding ligth on niche specialization and related problems. *Metabolism : temperature curves* represent another means of interpreting habitat organism relationships since usually there is some connection between Q_{10}-values and the ranges of optimum temperature experienced by species in nature. One case of *seasonal acclimatization* of oxygen consumption has been reported. Optimum *developmental temperature* appears to be a characteristic of all the species living in a particular habitat — which is not true for the upper lethal temperatures of these species. A very striking phenomenon is the ability of some inhabitants of temperate beaches to carry on with developmental processes at subzero temperatures and even in a frozen condition.

2) pO_2

In the few species analyzed oxygen consumption conforms to pO_2 in the case of *Enoplus brevis*, assisted by the presence of haemoglobin in the muscles, down to very low values. Acclimatization of metabolism to low pO_2 is possible. No sign of an oxygen debt was detected. Close to anoxic conditions most species become immobile, but at least one species, *Paramonhystera wieseri*, turned out to be a true anaerobe, being equipped with very peculiar mitochondria.

3) *pH*

Resistance studies revealed close correspondence between lethal alkaline pH and maximum pH experienced by various species in their habitat. This indicates that there is very little « Excess » alkaline resistance, at least in the inhabitants of a subtropical beach.

4) *Salinity*

In littoral species resistance to salinity appears to be closely correlated with the extremes of concentration and dilution in that zone in which the species is maximally abundant. The rate of development is also adjusted to this ecological factor, being fastest at the average habitat salinity.

5) *Food*

The attraction of nematodes by specific food sources (aspects of « sensory ecophysiology ») has been studied, and the possible involvement of the amphids has been suggested. The classification of « feeding types » based on buccal structure has proven to be an ecological tool of some values, particularly in connection with the determination of oxygen consumption, since a fairly clearcut relationship could be established between feeding type and level of metabolism.

In summary it may be said that this field of nematology is wide open. Most studies have resulted in rather conventional findings but an analysis of the adaptations of nematodes to low pO_2 may prove to have implications of wider biological significance.

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ROUND TABLE DISCUSSIONS

summarized by

A. COOMANS, L. DE CONINCK and C. HEIP

The round table discussions at the end of the meeting were summarized from tape recordings that were not always clear and voices could not always be identified. Therefore we decided to give the main ideas that were expressed and were proposed or accepted by all or a majority of the participants, without reference to any person. We hope that this summary is a true reflection of what was said with many more words.

THE ONTOGENY OF TAXONOMIC CHARACTERS

A list of important characters of which the ontogeny is known or should be known was established. The adult is only one stage in the life cycle and study of juveniles can lead to the establishment of phyologenetical lines ; but only a few studies have taken juveniles into account, despite the fact that ontogenetic investigations are necessary to answer questions about homologies, the direction of evolution and the distinction between primitive and advanced characters.

Important taxonomic characters are to be found in : *a*) the cephalic region with its sense organs and the stoma region ; *b*) the reproductive system ; *c*) the tail region. With these are connected the presence and number of cephalic setae, the anterior sense organs and the ontogeny of the mouth cavity. There is little information on the cells that form these structures and much work on ultrastructure remains to be done. The place and form of the amphids may change during ontogeny and even the number of lips. The position of the excretory pore changes as well and is often different in juveniles. The number of cells forming the intestine, the number of body and (if present) adhesive setae and the body annulation may all change during ontogeny. Culture methods will be invaluable in this kind of problems.

Because the spicular apparatus is already developing in the fourth juvenile stage mistakes can be made by describing these as adult males. Moreover, abnormal individuals may occur, hence the danger of descriptions based on one or a few specimens.

HOMOLOGIZATION OF STOMA STRUCTURES

The use of phylogenetically loaded terms poses problems for the practising taxonomist who needs to describe these structures and can not wait until the embryological data are available. For instance, the position of the teeth may be useful but they occur in different regions and in practice it is often difficult to determine exactly in which. It may be necessary to set up specific criteria to designate the cheilostome in each major taxon. The use of descriptive terms instead of terms referring to ontogenesis or phylogenesis is certainly useful in many instances when the origin of a particular structure is uncertain.

The terminology proposed by Steiner in 1933 for the different regions of the stoma in Rhabditida is difficult to use for other groups because of our limited knowledge about homologies and because of several errors made in the past. Homologies should be determined according to Remane's criteria. The most anterior part, immediately behind the oral opening, is lined with a cuticle that is very similar to the body cuticle and has basically the hexaradial symmetry of the lip region. This part could be referred to as cheilostome (as Steiner proposed), or perhaps vestibule or lip cavity. Although originally and still usually confined to the lip region, the cheilostome may extend further backward and on its wall may develop denticles or tooth-like structures of variable shape and number according to the group or species. The cheilostome joins that part of the alimentary channel that is derived from the stomodeum and differentiated as anterior feeding apparatus. The latter part has been given various names, partly because of the very different shape it can have in relation with the feeding habits or with the group, e.g. stoma (then including the cheilostome), buccal cavity (sometimes also including the cheilostome), modified anterior feeding apparatus, oesophastome, oesophagostome (an emendation of the previous name) or simply mouth cavity.

Since embryological and ultrastructural data are still scanty the practising taxonomist often cannot decide for certain what are homologous structures, therefore some practical criteria are needed for each major taxon that enable us, for the time being, to refer to specific parts of the stoma.

PHARYNX OR OESOPHAGUS?

The structure which in nematodes is designated most frequently by the word oesophagus (Gr. oesos = will transport ; phagos = food) is called pharynx in related groups. In the terminology of Remane, a pharynx is a predominantly muscular structure whereas an oesophagus is not. When both structures are present, as in Annelids and Molluscs, the pharynx is the more muscular part whereas the oesophagus is the more glandular part. In a more restrictive sense the word pharynx has been used to designate the anterior area of the oesopgahus, a region that might be called also the oesophagostome of modified anterior feeding apparatus, lying between the cheilostome and the oesophagus (see above). Pharynx and oesophagus are both borrowed from the vertebrate literature in which pharynx is used for the upper region of the oesophagus.

It was noted that many nematologists now think that the term pharynx might be more appropriate but that further discussion will be necessary before an agreement will be reached.

SYSTEMATICS AND ECOLOGY

There are still conflicts between those taxonomists that want to base their classification on practical grounds and those that try to base it on phylogenesis. Whatever system is adopted it should be clearly stated. Even in a phylogenetic system the available information may be insufficient for establishing monophyletic groups and hence some taxa may be made for practical reasons, for the time being. A classification that reflects phylogeny as much as possible is to be preferred because it is the most interesting and has a predictive quality. However, this implies careful studies of ontogeny, comparative morphology and others to evaluate the different characters and to trace the homologies.

Taxonomists describing new taxa should be aware of the fact that their findings are not only useful for the practising nematologist but that their descriptions should also deal with characters that may be important for a phylogenetical study later on, rather than just deal with the diagnostic features of new species. On the other hand, the practical problems should also be kept in mind and when e.g. new taxa are based on characters that can only be observed with an electron microscope, this will give problems to most practicing nematologists. It was nevertheless generally agreed upon that descriptions of new taxa should give as much information as possible in order to be useful for different disciplines. Furthermore, it was stressed that also the ecologist is better off with a natural classification than with an artificial one, since the evolution of the animal groups parallels that of the ecosystems.

Comprehensive books have inspired nematological work in the past and will continue to do so. Keys are necessary and very helpful if well made. Dichotomous ones are most widespread and can lead to quick identifications. Tabular keys are more elaborate and give more information. Pictorial keys are attractive also to non specialists and help to avoid confusion about the correct interpretation of the terminology. Here again one can try to follow the different steps of the phylogenetic classification or try to make the easiest and most practical key based on the most obvious characters. In the latter case however, the result has always to be verified with the relevant literature.

It was felt very useful especially for beginners to establish a guide with data to be considered when a new species is described or when a poorly known species is redescribed (see Addendum II). Of course a list of such data has to be adapted to each group and whenever new things are discerned. In using a guide, list or table attention will be given to many details that would otherwise be overlooked. It would be a great help for all taxonomists if at least one species of each genus would be described in as much detail as possible. This could serve as a reference and then only the difference with that species would have to considered in other descriptions of species belonging to that genus.

Since the meiofauna is considered more and more as composed of key environmental indicators, more and more people will become involved with identification of nematodes, but only few are real specialists now. Good pictorial keys might be a help for those less trained people, but identification up to generic and certainly up to specific level is difficult even for specialists. The problem is that governmental agencies sponsoring such research want us to detect changes in faunal composition and that they require quick answers. This is nearly impossible. Under these circumstances the identification up to the genus level is useful. Unfortunately, nematodes have not attracted many people because of the difficulties in identifying them and this is distressing since they are the dominant group in the marine benthos.

THE TERMINOLOGY OF BODY REGIONS

The terminology of body regions proposed by De Coninck in 1942 and 1965 (Fig. 1) could be a basis for a discussion. Whereas axes can be readily defined, this is not so for areas and here opinions differ. The terms subventral and subdorsal are used in a very general way by many nematologists for an area somewhere between lateral and ventral resp. lateral and dorsal. In this general sense a subventral or subdorsal position is not clearly defined as it is in De Coninck's scheme. It may be easy for such structures that shift in position throughout the body length and for those where the exact position cannot be defined. The use of unprecise terms may however lead to confusion and whenever the position of structures can be exactly defined, precise terms are necessary to enable detailed comparisons. Areas could be delimited by the axes that border them, e.g. the ventral-subventral area (left and right), the ventral-lateroventral area..., or the median axis of the structure could be used for the whole area ; however, the fact that nematodes are bilaterally symmetrical in general and tri- or hexaradially symmetrical in the anterior region complicates the story. The bilateral symmetry and the triradial one should not be confused with each other. The main problem seems to be the term subventral, which is often used in a very general way for structures situated somewhere between lateral and ventral. It is commonly used because it is a short term, but since it is used for positions « not exactly » ventral or « almost » ventral, it is not a very precise term in this sense. In the scheme of De Coninck it is clearly defined (Fig. 1). It was suggested that a proposition should be worked out and then further discussed and amended by practising nematologists until a general agreement can be reached (see addendum I).

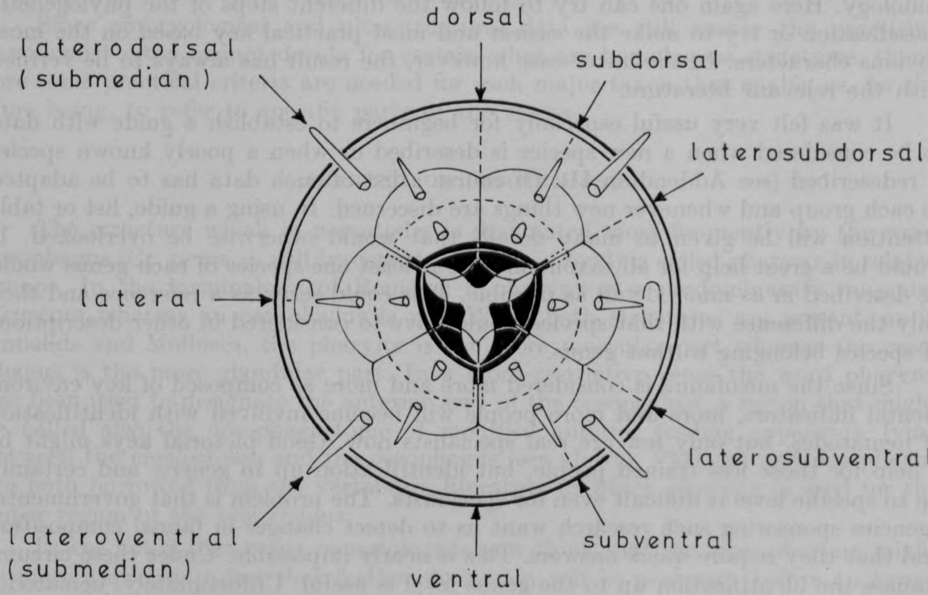

Fig. 1. — Terminology of body regions (after De Coninck, 1942, 1965).

Several other terms were discussed as well. The following terms were considered as synonyms for the region between the anterior end of the body and the cardia or oesophago-intestinal junction : « *neck-region* », « *cervical region* », « *oesophageal region* » and « *pharyngeal region* ».

Male nematodes have a cloaca, whereas in females this is exceptional. Hence, females generally have an anus whereas males have a cloacal opening. Most participants were nevertheless in favour of the use of terms as « anal diameter », « preanal », « ad-anal », « postanal », etc. for males as well.

The secondary sexual characters that are often present in the posterior region of males are variously called papillae, genital papillae, supplements or supplementary organs. Although they may be of different origin, they can be commonly called

« *supplements* » or « *supplementary organs* » when also their position is indicated, e.g. preanal, adanal, postanal, medioventral, subventral, etc.

The term *lateral field* is sometimes used in two different meanings ; it should be restricted to the differentiated cuticular region above the lateral chord ; the latter term should only be used for the epidermal (hypodermal) chord.

Although *hypodermis* is widely used in nematology, *epidermis* is more correct. Also entomologists more and more use epidermis instead of hypodermis for the cellular layer underneath the cuticle.

The terminology of the cephalic sense organs was also discussed and De Coninck's terminology was generally accepted. According to this there are : a first circlet of six inner labial papillae, a second circlet of six outer labial papillae or setae and a third circlet of four cephalic papillae or setae ; the second and third circlet may unite and form a single circlet of ten papillae or setae.

COLLECTIONS

The establishment of reference collections deposited at musea and other public institutions with type and/or other specimens was emphasized. This allows future revisions and corrections.

Private collections should be transferred to public institutions where they are cared for and available to those interested. Type specimens belong to science, not to persons ! The rules of zoological nomenclature should make it obligatory to deposit type specimens in public institutions. Acceptance of a paper describing new species by a journal should depend on deposition of type specimens in at least one major public collection.

The exchange of identified material is also very important and should be stimulated. It was felt useful that a circular should be sent to all taxonomists in order to know where the collections of practising as well as retired or deceased nematologists are.

A discussion was held about what should be done about the species described by Allgén, whether they should be redescribed on the base of the slides from his collection and new material from the type localities, or whether they should be ignored. Bad descriptions of new species are a nuisance to all people that have to deal with them afterwards. Many of Allgén's species are in that position. A number of these can not be identified and were or will have to be put under « species inquirendae », so that they no longer will confuse anybody. However, when it is possible to redescribe such species with the aid of topotypes and a neotype can be selected, it was considered preferable to do this rather than discounting the older species as « inquirenda ». Even if there is still some doubt about the identity of topotypes and the original species it is still better to validate the older name rather than adding a new name to the list.

Since Allgén described many new species from many different families it seems impossible for one man to revise them. For this but also for other revisions cooperation should be encouraged. Agreements should be made amongst specialists to avoid that some groups would be revised several times and others not at all, so that everybody could benefit from it and there would be no competition. In this respect it would also be useful to organize a workshop where specialists and other interested people could come together with material, study it and discuss about it. Higher groupings and overall classification of nematodes should also be done by a group of specialists that cooperate and no longer by one individual.

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ADDENDUM I

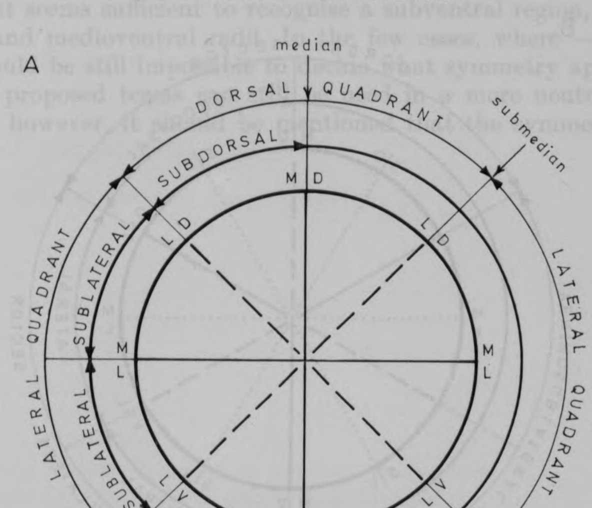
A PROPOSAL FOR A MORE PRECISE TERMINOLOGY OF THE BODY REGIONS IN THE NEMATODE

by

A. COOMANS

During the discussion on terminology of the various body regions of a nematode it was suggested that a proposition should be worked out as a basis for further discussion and amendation. The scheme proposed here is a further development of that of De Coninck (1942 & 1965, see Fig. 1 in the summary of the symposium discussions). It recognises the two fundamental symmetries of the nematode body plan and it is important that the terminology for both should not be confused.

BILATERAL SYMMETRY



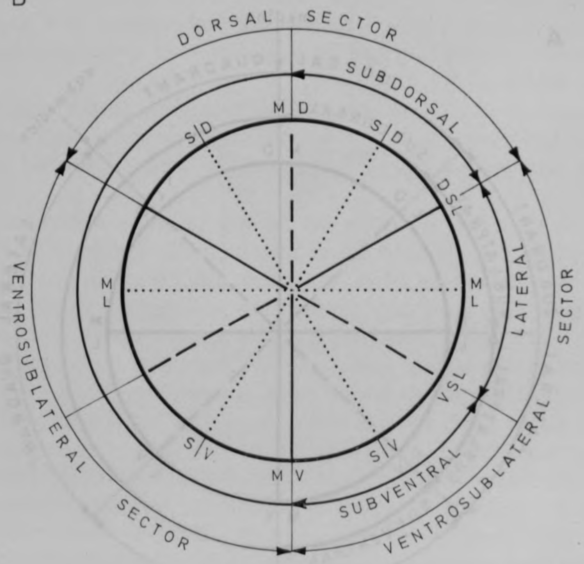
MD = mediodorsal
ML = mediolateral
MV = medioventral
LD = laterodorsal
LV = laterodorsal

In the bilaterally symmetrical body plan (Fig. A) there are four equal areas that could be called quadrants : two lateral, one dorsal and one ventral. The quadrants are limited by the laterodorsal and lateroventral radii and divided into two equal halves by the mediolateral, mediodorsal and medioventral radii. The regions delimited by all these radii could be referred to by adding the prefix « sub ». In this way each quadrant is composed of two equal subregions (« octants »), in total four sublateral, two subdorsal and two subventral. With these terms all the bilateral structures can be situated.

The triradially symmetrical structures of the nematode need a somewhat different terminology and unfortunately but inevitable somewhat different definitions for the similar terms as in the bilateral symmetry. Here there are three equal areas (Fig. B) : one dorsal and two ventrosublateral ones, delimited by the two dorsosublateral and the medioventral radii. They could be called sectors to distinguish them from the quadrants. The dorsal sector of the triradial plan is larger than the dorsal quadrant of the bilateral plan ; it can be subdivided in two equal subdorsal sectors that are also larger than the subdivisions of the dorsal quadrant. The two ventrosublateral sectors can be subdivided in a lateral and a subventral sector each. The lateral sector is smaller than the lateral quadrant, while the subventral sector is larger than the subventral half of the ventral quadrant.

TRIRADIAL SYMMETRY

B



MD = mediodorsal
ML = mediolateral
MV = medioventral
SD = subdorsal
SV = subventral
DSL = dorsosublateral
VSL = ventrosublateral

All this may appear rather confusing and complex at first sight, but taken into account that the triradial symmetry applies only to the pharynx or oesophagus and to the lip region, while the bilateral symmetry applies to all the other structures, this objection is easily discarded as not being of practical importance.

It is clear that exact positions can only be indicated with the radii, e.g. the position of the anterior sense organs of the nematode, the position of the pharyngeal or oesophageal teeth and gland outlets can be easily and unambiguously referred to. Structures that have not such exact locations can be only situated in a sector. When using the proposed schemes, this position can however be reasonably well indicated, e.g. longitudinal body setae or papillae are laterodorsal and lateroventral in position when present as four rows, but when they occur in eight rows they are subdorsal, sublateral (dorsally and ventrally) and subventral in position. Body pores connected with the lateral chords are sublateral in position, when connected with the ventral chord they are subventral or medioventral.

Some of the terms proposed, e.g. ventrosublateral are not yet commonly used and rather long, perhaps a shorter and easier term could be found that is equally informative.

It would already be a step forward if the so commonly used term subventral would get a more precise meaning than « somewhere between lateral and ventral ». In the scheme's proposed above it is precisely defined in the triradial plan as (1) the ventral half of each ventrosublateral sector, it applies e.g. to the two subventral lips when six lips are present ; (2) the radius in the middle of this region, that is in the middle between the ventrosublateral and the medioventral radii. In the bilateral plan it seems sufficient to recognise a subventral region, delimited by the lateroventral and medioventral radii. In the few cases, where — after a detailed study — it would be still impossible to decide what symmetry applies to a certain structure, the proposed terms can still be used in a more neutral way. To state things clearly, however, it should be mentioned that the symmetry plan was not detected.

ADDENDUM II

DATA TO BE CONSIDERED IN DESCRIPTIONS OF NEW SPECIES OR REDESCRIPTIONS OF POORLY KNOWN SPECIES

Species :

Locality :

Habitat :

Material :

Number of	juveniles				♀♀	♂♂
	1	2	3	4	— eggs +	

Measurements of the types :

L a b c

Formula of Filipjev, 1921

Averages and extremes of the population.

Description :

	Dimensions	Figures
— Habitus		×
— Cuticle		
. smooth — annulated		
. lateral field (width relative to corresp. body diam.)		
. pores : number and distribution of epidermal glands in lateral fields		
— structure of gland outlet		
— ventrally		
— other (sensorial)		
— Cephalic region		
. general shape		×
. cephalic helmet : shape		
extern — intern		
. sensorial organs :		
(1) internal labial setae — papillae		
external labial setae — papillae		

cephalic setae — papillae
subcephalic setae
(2) amphids : general form
size relative to ceph. diam.
apertura : length-width
dist. ant. extrem.
corpus gelatum
fovea : termin. fil.
fusus : cil. struct.
sexual dimorphism
juv. — ad. morphogenesis

— Buccal cavity
. general structure
. cheilostome : lips — number and structure
— anterior appendices
— cuticularisations
. oesophagostome : teeth — hollow or solid
denticles
subdivisions
. musculature (protractors — retractors)

— Oesophagus = Pharynx
. general structure
. presence or absence of radial canals
. musculature
. glands : nuclei
outlets
. bulb(s)
. cuticularisation of lumen and in bulb(s)

— Nerve-ring
. measurement : centre of nerve-ring relative to oesoph. length
. ganglia? in front of and behind nerve-ring
. metanemes (3) : nervous elements in body-musculature near lateral chords

— Ventral gland
. excretory pore
. ampulla
. position relative to buccal cavity — to nervering or oesoph. length

— Cardia
. cell number
. shape

— Intestinal tract
. cell number
. cell differentiation
. rectum
. contents

— Reproductive system
. female gonad(s) ×
number
position : anterior, posterior
relative to intestine (4)
outstretched or reflexed
germinative zone
differentiation zone
oviduct
receptaculum seminis
uterus
egg(s)
vagina
vulva — lips — epiptygma
glands
Demanian system (in Oncholaimids) :
structure, type (5)
musculature
. male gonad(s) ×
number : single — double
position relative to intestin
germinative zone
differentiation zone
spermatozoa
gonoduct
seminal vesicle
ductus deferens
ductus ejaculatorius
associated glands
. copulatory system
spicule(s) : structure ×
size : arc — cord (relative to anal diam. and to tail length)
single
double : equal — unequal
musculature
gubernaculum : structure ×
caudal apophyse(s)
single — double
musculature
accessory organs : sensorial
glandular
cuticularisations
structure — number
size
distribution
copulatory body-musculature

— Anal region
. musculature

— Tail region
  . general shape
  . size (relat. anal diam.)
  . sensorial organs
  . caudal glands : number
    position
  . spinneret : structure

— Larval morphology and measurements not to be neglected !

Discussion and remarks :

  . morphology (general)
  . systematics (differences from most related species — eventually genera)
  . ecology

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(1) Cfr. De Coninck, 1942 or 1965 ; *Traité de Zoologie* (éd. Grassé), 4(2).
(2) Cfr. Riemann, 1971 ; *Z. Morph. Tiere* 72, 46-76.
(3) Cfr. Lorenzen, 1979 ; *Zoologica Scripta*. Vol. 7, 175-178.
(4) Cfr. Lorenzen, 1979 ; *Z. zool. Syst. Evolut.-forsch.* 16, 108-115.
(5) Cfr. Rachor, 1969 ; *Z. Morph. Ökol. Tiere* 66, 87-166.
× : desired figures.

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Koninklijke Belgische Vereniging voor Dierkunde

V.Z.W.

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Annales
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(V. Z. W.)

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Les Annales de la Société royale zoologique de Belgique sont destinées à publier des travaux originaux ou des mises au point, réalisés ou présentés par des membres de la Société, dans les domaines de la Zoologie et de la Biologie animale.

Les textes sont soumis à l'appréciation du Comité de Rédaction.

Toutefois, les opinions exprimées par les auteurs leur sont propres et le Comité de Rédaction n'en assume aucunement la responsabilité.

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Het ligt in de bedoeling van de Annalen der « Société royale zoologique de Belgique » oorspronkelijke bijdragen, betreffende de Dierkunde of de Biologie der Dieren, op te nemen uitgaande van de leden der Maatschappij of door deze voorgedragen.

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Juillet 1979 (*Communication reçue le 17 mai 1978*)

LA GLANDE NIDAMENTAIRE ACCESSOIRE DE *SEPIA OFFICINALIS* L. : ANALYSES BIOCHIMIQUES DES PIGMENTS DES BACTÉRIES SYMBIOTIQUES

par

C. VAN DEN BRANDEN (1), A. RICHARD (2),
J. LEMAIRE (3) et W. DECLEIR (1)

RÉSUMÉ

L'examen ultrastructural des cellules de l'épithélium des glandes nidamentaires accessoires permet de mettre en évidence un cycle sécrétoire et la présence de bactéries dans les lumières tubulaires. Il y a corrélation entre l'évolution génitale, la coloration des glandes et le nombre de bactéries symbiotiques intra-tubulaires. Ces observations et les résultats biochimiques montrent que l'élaboration des différents pigments dont la SEPIAXANTHINE (pigment caroténoide orange), des glandes nidamentaires accessoires résulte d'un mécanisme métabolique particulier des bactéries symbiotiques, suite à une sécrétion de la glande. Le mode d'infestation et la spécificité de ces bactéries sont dis cutées.

An electron microscopic study of the accessory nidamental glands from *Sepia officinalis* L. shows a secretory cycle in the epithelial cells and the presence of bacteria in the tubules of the gland. A correlation between sexual maturity, the color of the gland and the total number of symbiotic bacteria can be demonstrated. A biochemical study shows that the coloration of the gland is due to several carotenoid pigments. The most important of these is an orange-red xanthophyll that has been called SEPIAXANTHINE. It is probably formed in the bacteria as a result of the secretory activity of the epithelial glandular cells. This whole mechanism and the role of the bacteria and pigments need further research.

INTRODUCTION

En nous basant sur de nombreuses observations (Richard 1966b, 1967, 1971), nous avons pu établir (tableau 1) un parallélisme entre la maturation ovocytaire et l'évolution tinctoriale des glandes nidamentaires accessoires chez la seiche (Mollusque Céphalopode). Comme Pierantoni attribuait dès 1918 cette couleur à des bactéries symbiotiques, nous y avons recherché la localisation du pigment que nous avions précédemment proposé de dénommer *Sepiaxanthine* (Decleir et Richard, 1972).

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TABLEAU I

Evolution tinctoriale des glandes nidamentaires accessoires (critère de maturation sexuelle)

Couleur de la glande nidamentaire accessoire	Stades d'activité ovarienne
Incolore à blanc	Repos sexuel : st. 1 et 2 mitoses ovogoniales et prophase de méiose
Blanc-crémeux	Début d'activité : st. 3a (Prévitellogenèse : disposition des cellules folliculaires à la périphérie de l'ovocyte I)
Beige	Prévitellogenèse : st. 3b (Disposition des cellules folliculaires en cordons intraovocytaires)
Jaune	Vitellogenèse : st. 4 (Début d'activité sécrétoire des cellules folliculaires)
Orangé	Vitellogenèse : st. 5
Corail	Maturité sexuelle totale : st. 6 (Émission des globules polaires)

MATÉRIEL ET TECHNIQUES

a) *Matériel*

Les glandes nidamentaires accessoires ont été prélevées sur des seiches femelles adultes, récoltées durant l'expédition « Céphalomanche » (*), ou provenant de lots d'élevage selon la technique mise au point par Richard (1966a, 1975). Les glandes sont fixées immédiatement pour les observations microscopiques ou congelées à — 20° C pour les études biochimiques.

b) *Techniques microscopiques*

1. *Photoniques*

Après dissection, les glandes nidamentaires accessoires sont fixées au liquide de Bouin-Hollande, incluses à la paraffine après passage à l'alcool butylique. Les coupes à 7 μ, sont colorées par l'hématoxyline de Groat — picro-indigocarmin ou le trichrome de Prenant.

2. *Electroniques*

Les fragments de glandes (1 mm³) sont préparés selon la méthode suivante :

— fixation au glutaraldéhyde à 6 % dans un tampon 0,067 M de cacodylate

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(*) Campagne C.N.E.X.O.-I.S.T.P.M., Avril 1975.

de sodium, pH 7,4, pendant 4 heures à 4° C (le glutaraldéhyde est purifié avant l'usage par absorption au charbon et distillation sous vide : FAHIMI et DROCHMANS, 1965 ; ANDERSON, 1967)

— lavage dans le même tampon cacodylate, contenant 7,5 % de saccharose, pendant trois fois 15 minutes à 4° C

— post-fixation à l'acide osmique à 2 % dans un tampon 0,038 M acétate de véronal, pH 7,4 contenant 4 % de saccharose, pendant 90 minutes à 4° C (CAUFIELD, 1957)

— puis après lavage dans le même tampon acétate de véronal, les fragments, déshydratés dans l'acétone à température ambiante, sont inclus en résine epoxy Durcupan et coupés au microtome Reichert OMu2 (épaisseur 500 à 600 Å). Les coupes sont contrastées à l'acétate d'uranyle (WATSON, 1958) pendant 10 minutes et aux sels de plomb (REYNOLDS, 1963) pendant 20 minutes dans une atmosphère libre de CO_2. Les coupes sont examinées au Siemens Elmiskop Ia.

c) *Techniques biochimiques*

1. *Isolement des granules de la glande nidamentaire accessoire*

Les glandes sont homogéneisées dans un tampon phosphate (tampon 0,01 M à pH 8, 0,5 % KCl et 0,1 % $MgCl_2$) à l'aide d'un homogénéiseur Virtis (trois fois 3 minutes à 30.000 tours/minute, 4° C). L'homogénat est centrifugé pendant 10 minutes à 10.000 g à 4° C. Le surnageant « orange » contient les granules.

On peut également libérer les granules des lumières des tubules glandulaires : le tissu, coupé en petits fragments est placé dans une petite quantité de tampon phosphate, agité pendant 1 heure et centrifugé comme l'homogénat.

2. *Gradient de densité*

Des gradients discontinus de saccharose sont préparés manuellement (1 ml de saccharose à 66 %, 60 %, 50 %, 40 % et 30 %). Sur chaque gradient, 0,5 ml d'homogénat glandulaire est séparé par centrifugation pendant 1 heure à 140.000 g à 4° C dans un rotor du type Swinging bucket SW 50.1.

Pour étudier l'effet de l'enzyme protéolytique (la pronase), la procédure suivante a été adoptée : l'homogénat de la glande est séparé sur un gradient discontinu de saccharose, centrifugé pendant 30 minutes à 17.000 tours/minute. La fraction la plus orange est isolée, sédimentée et reprise dans le tampon phosphate. Après 6 jours de traitement à la pronase à 37° C, cette fraction est de nouveau sédimentée pendant 30 minutes à 45.000 tours/minute. Le culot de sédimentation est repris par le tampon phosphate et mis sur un gradient discontinu de saccharose dans les mêmes conditions que l'homogénat non-traité.

L'effet du traitement par ultrasons a été étudié en soumettant l'homogénat pendant 15 minutes à des ondes ultrasonores d'amplitude 20 μ, puis séparé sur un gradient discontinu de saccharose dans les mêmes conditions que l'homogénat non-traité.

Après centrifugation les différentes bandes colorées sont collectées avec une pipette Pasteur et mises à sédimenter pendant 1 heure à 145.000 g.

3. *Isolement des pigments de la glande nidamentaire accessoire*

Afin d'isoler les pigments de la glande nidamentaire accessoire l'homogénat est soumis aux ultrasons pendant 20 minutes et centrifugé (145.000 g) pendant 1 heure à 4° C. Le culot sédimentaire rouge est dissous dans le mélange chloroforme-méthanol

(1/1). La division en épiphase et hypophase se fait selon les méthodes classiques. Le coefficient de répartition est déterminé selon Krinsky (1963). La séparation et la détermination des valeurs R_f des différents pigments épiphasiques et hypophasiques se font sur des couches minces de silicagel dans le système éther de pétrole-acétone (98/2) ou le système chloroforme-méthanol-H_2O-NH_3 (80/40/4/3). La position des maxima spectraux a été déterminée avec le Cary 118 spectrophotomètre.

La concentration des pigments est déterminée à l'aide de la formule :

$$X = \frac{E\ .\ Y}{E^{1\,\%}_{1\,\mathrm{cm}}\ .\ 100\,Z}$$

avec : X : concentration du pigment en g/g de poids sec
Z : poids sec de la glande en g
Y : volume du solvant en ml
E : extinction
$E^{1\,\%}_{1\,\mathrm{cm}}$: extinction spécifique du β carotène
(valeur de D.O. pour la solution à 1 % dans l'hexane = 2.500)

d) *Culture des bactéries*

Un milieu de culture solide, contenant 1 % de tissus de seiche homogénéisés (muscles du manteau et foie), 0,4 % de glucose et 2 % d'agar dans l'eau de mer artificielle a été utilisé. Les plaques ont été inoculées avec un fragment de glande nidamentaire accessoire, prélevée de façon stérile. Les plaques sont incubées à température ambiante dans la semi-obscurité. Les caractéristiques des bactéries ont été déterminées avec les méthodes classiques (Buttiaux, Beerens et Tacquet, 1974).

RÉSULTATS

1. *Morphologie des glandes nidamentaires accessoires*

Les glandes nidamentaires accessoires de la seiche se situent sur la face ventrale et s'ouvrent dans la cavité palléale (Pl. I). Chez la jeune seiche, les glandes nidamentaires, déjà différenciées (Lemaire, 1972), se présentent sous la forme de rosettes de faible épaisseur (Pl. I, fig. 1). En coupe (Pl. I, fig. 4), la glande est formée par

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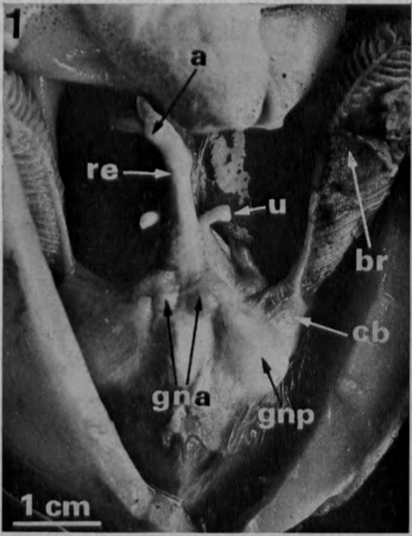
PLANCHE I

Fig. 1 : Vue ventrale d'une jeune seiche. Les glandes nidamentaires accessoires sont de couleur « blanche ».
Fig. 2 : Vue centrale d'une seiche dont les glandes nidamentaires se colorent (couleur « beige »).
Fig. 3 : Vue ventrale d'une seiche à maturité sexuelle : les glandes nidamentaires accessoires bien développées, sont de couleur « corail ».
Fig. 4 : Disposition des glandes nidamentaires principales et accessoires en coupe sagittale (longueur de la seiche : 25 mm, glandes nidamentaires accessoires « non colorées »).
Fig. 5 : Détail des glandes nidamentaires accessoires « non colorées ».
Fig. 6 : Détail des glandes nidamentaires accessoires fonctionnelles (couleur « orangé »).

a : anus ; b.c. : bord ciliaire ; br : branchie ; c.b. : cœur branchial ; c.p. : cavité palléale ; F. : foie ; g.n.a. : glande nidamentaire accessoire ; g.n.p. : glande nidamentaire principale ; g.o. : glande de l'oviducte ; o.e. : orifice excréteur des glandes nidamentaires principales ; re. : rectum ; t. : tubule ; u. : orifices urinaires.

PLANCHE I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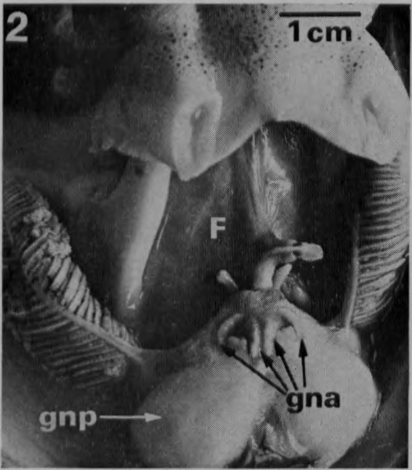
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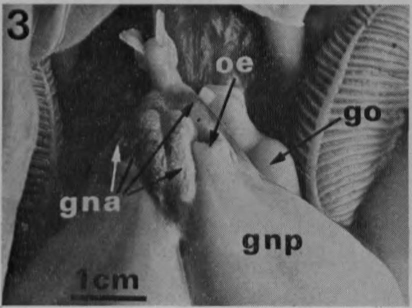
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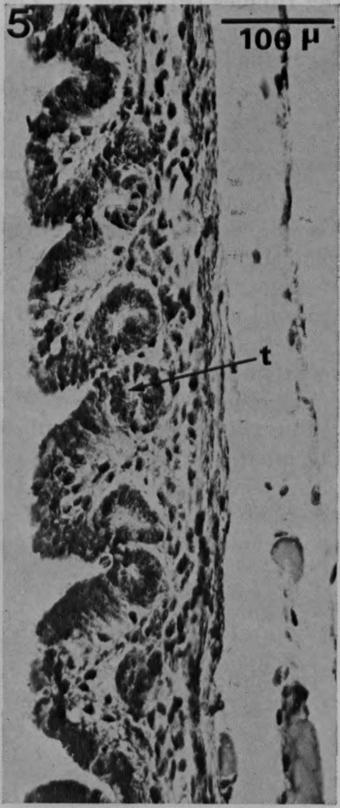
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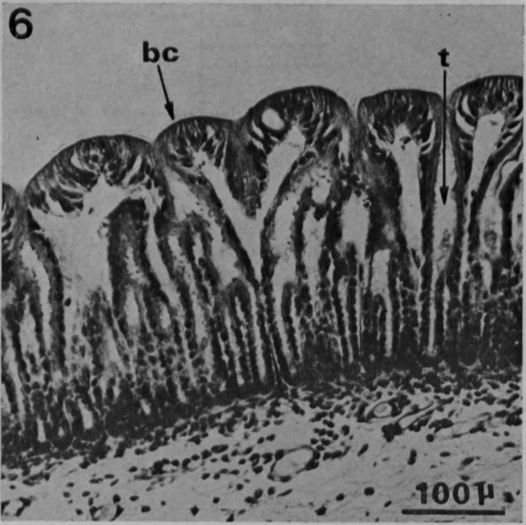
6
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des replis de l'épithélium de la cavité palléale. Ceux-ci s'organisent progressivement en tubules (Pl. I, fig. 5). Les glandes qui forment alors quatre lobes augmentent en épaisseur et viennent coiffer les extrémités antérieures des glandes nidamentaires principales (Pl. I, fig. 2).

La croissance des glandes se poursuit : on y distingue de nombreux tubules (Pl. I, fig. 6). Elles s'allongent et, chez la seiche femelle adulte, elles se présentent sous forme de quatre masses oblongues, situées de part et d'autre des orifices excréteurs des glandes nidamentaires principales (Pl. I, fig. 3).

Parallèlement à cette évolution, on retrouve dans les glandes nidamentaires accessoires les différentes étapes tinctoriales déjà citées. Un examen des cellules de l'épithélium glandulaire permet de mettre en évidence un cycle sécrétoire. Dans ces cellules, on remarque de nombreuses mitochondries à matrice dense et un ergastoplasme abondant et actif. De nombreux saccules golgiens élaborent des granules de sécrétion de diamètre variable, pouvant atteindre 1,5 μ de diamètre (Pl. II), qui sont émis dans la lumière des tubules (RICHARD et LEMAIRE, 1978, sous presse). Ces cellules, étroitement liées entre elles, sont bordées par de nombreuses microvillosités (Pl. II). Des touffes de cils enchassés en disposition régulière jouent probablement un rôle de brassage actif dans la lumière tubulaire. Entre ceux-ci, on note la présence de sections de 0,5 à 1 μ dont la structure permet de penser qu'il s'agit de bactéries. Celles-ci sont en nombre variable ; il semble qu'il existe une corrélation entre leur abondance, le développement de la glande et l'activité sécrétrice de celle-ci.

2. *Résultats biochimiques*

a) *Gradients de densité*

Après ultracentrifugation sur un gradient discontinu de saccharose l'homogénat de la glande nidamentaire accessoire est séparé en 7 fractions (Fig. 1).

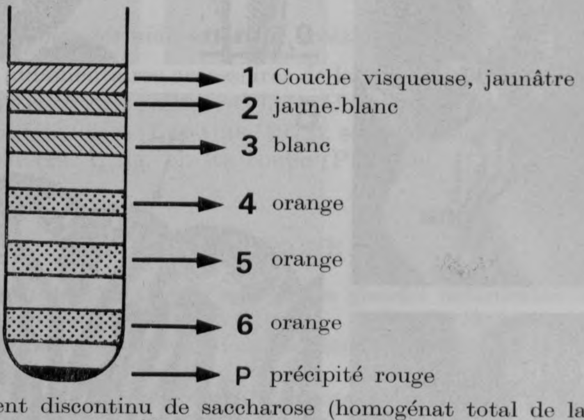


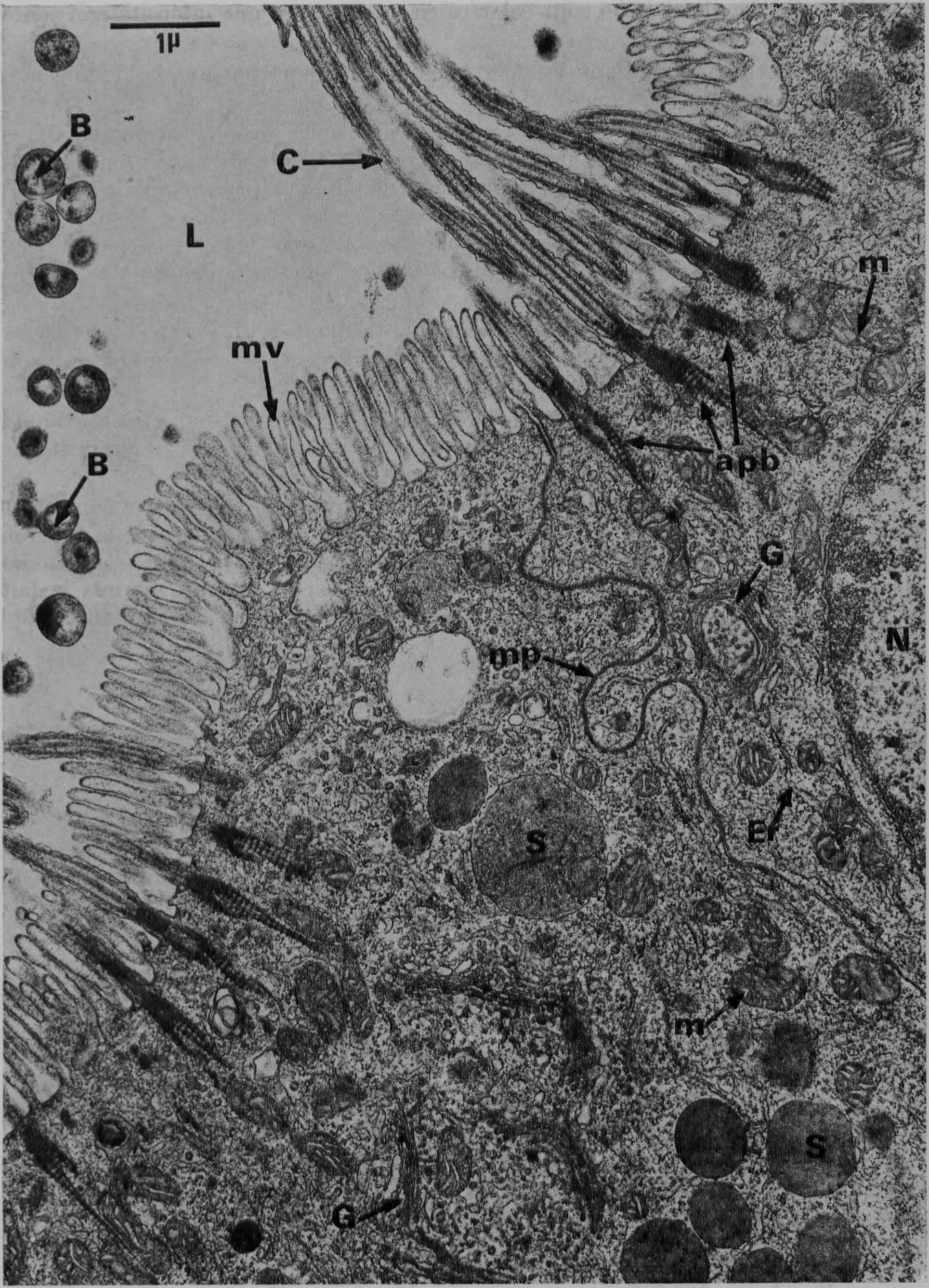
Fig. 1. — Gradient discontinu de saccharose (homogénat total de la glande nidamentaire accessoire).

PLANCHE II

Glandes nidamentaires accessoires de seiche (L = 80 mm) de couleur « beige » en début d'activité sécrétoire. Dans la lumière, on note la présence de quelques bactéries entre les touffes de cils (× 15.000).

a.p.b. : appareils parabasaux ; B. : bactérie ; C. : cils ; Er. : ergastoplasme ; G. : Golgi ; L. : lumière tubulaire ; m. : mitochondrie ; m.p. : membrane plasmique ; m.v. : microvillosités ; N. : noyau ; S. : granules de sécrétion.

PLANCHE II



La fraction 1 est une couche visqueuse jaunâtre claire et la fraction 2 est une solution claire jaune-blanc. Les fractions 3 à 6 sont granulaires. La fraction 3 est blanche et les fractions 4 à 6 sont colorées en orange avec une intensité croissante de 4 à 6.

Le précipité rouge contient des débris de tissu et des particules très hétérogènes, trop tassés pour permettre une étude.

Un examen des fractions 3 à 6 a été réalisé au microscope électronique. Dans la fraction 6 la plus orange, les granules sont très homogènes, de dimensions variant entre 0,5 et 1 µ. Certains contiennent une masse de petits grains osmiophiles (Pl. III, fig. 3 et 4) ; d'autres, un petit nombre de grosses boules osmiophiles (Pl. III, fig. 1 et 2). Nous retrouvons des divisions régulières ainsi que des rétrécissements qui sont probablement des stades de division. La paroi des granules est toujours épaisse et présente souvent des aspects « chevelus ».

La fraction 5, moins colorée en orange que la fraction 6, est très hétérogène. Nous avons pu identifier au moins une dizaine de différents types de granules (quelques uns de ceux-ci sont figurés planche IV).

La fraction 4, très légèrement colorée en orange, contient un nombre limité de granules à corps osmiophiles, tandis que la fraction 3, blanche, ne contient que de rares granules ressemblant à ceux de la fraction 4.

Après traitement de la fraction 6 par une protéinase telle la pronase, on obtient sur gradient de densité, 3 fractions et un précipité (Fig. 2). L'examen de la fraction intermédiaire « orange vif » au microscope électronique montre que les granules après traitement à la pronase n'ont pas changé d'aspect général, hormis le fait qu'ils sont devenus plus clairs, probablement à cause de la décomposition des protéines.

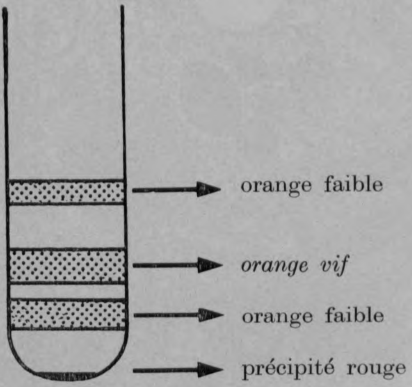


Fig. 2. — Gradient discontinu de saccharose (fraction 6 traitée à la pronase).

PLANCHE III

Aspects ultrastructuraux des « granules » de la fraction 6.

Fig. 1 : × 105.000	Fig. 3 : × 60.000
Fig. 2 : × 128.000	Fig. 4 : × 54.000

PLANCHE III

1

2

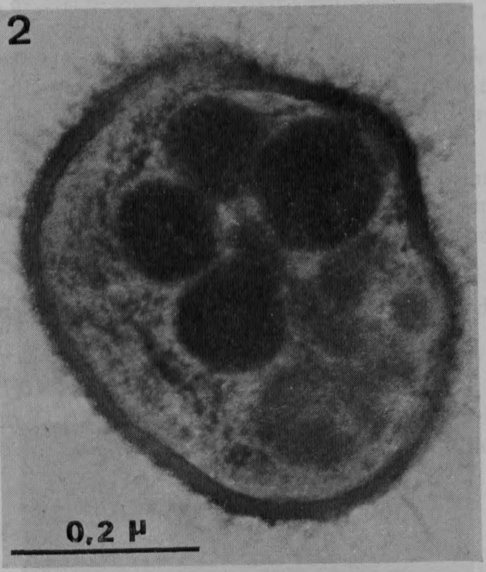


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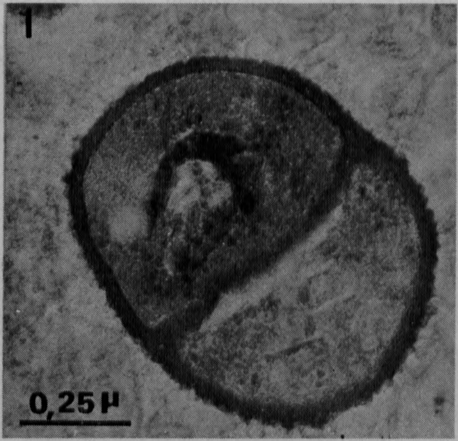
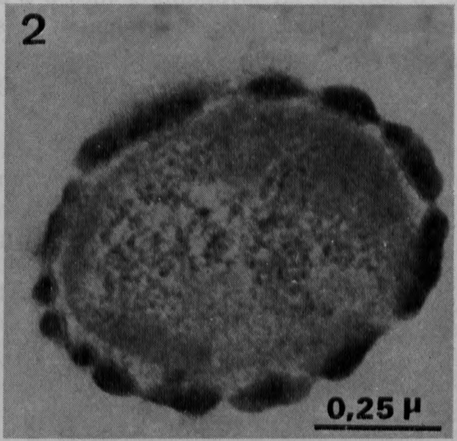
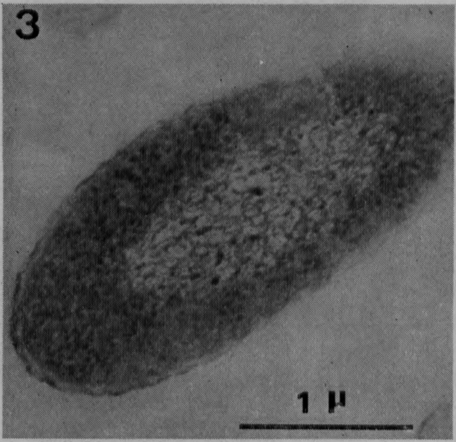
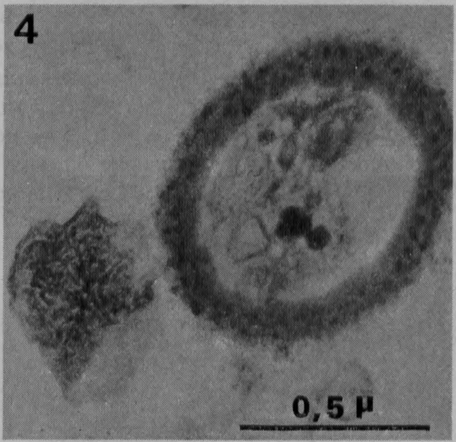
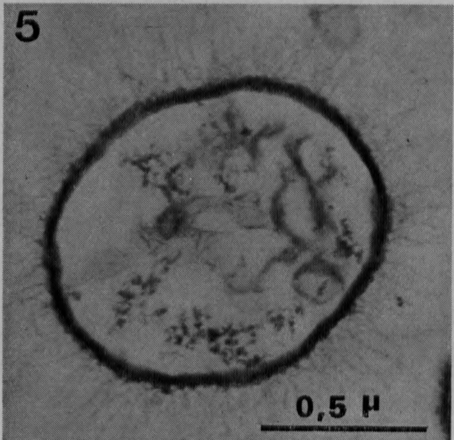
PLANCHE IV

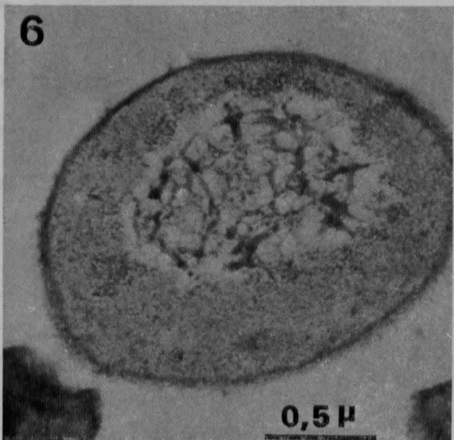












Après traitement aux ultrasons, les granules sont décomposés et on ne retrouve que les grains intragranulaires dans la fraction orange (Pl. V, fig. 1).

b) *Culture des bactéries de la glande nidamentaire accessoire*

Après 48 heures d'incubation, de petites colonies gris-blanc se sont développées sur un milieu composé de bouillon de seiche glucosé, à la température ambiante de 20° C. Les colonies ont un diamètre de 0,5 mm, une surface lisse avec un bord « entier ».

Après une semaine, certaines colonies prennent une couleur brune. Elles ne montrent pas de fluorescence sous la lumière ultraviolette, ni à 366 nm, ni à 254 nm. Elles consomment le citrate de sodium, ne forment pas l'indol et n'hydrolysent pas les protéines et les polysaccharides.

L'examen au microscope électronique montre la présence de deux types de bactéries :

— un type ressemblant aux granules de la fraction 6 (type 1, Pl. V, fig. 2)

— des bactéries en forme de bâtonnets de 2 à 3 μ de long et de 0,5 à 1 μ de large. Leur paroi est plutôt mince. Elles sont remplies de petits grains osmiophiles (type 2, Pl. V, fig. 2).

c) *Extraction et identification des pigments*

Après homogénéisation, séparation en phases et chromatographie en couche mince, nous retrouvons au moins 7 pigments différents, dont 4 sont épiphasiques et 3 hypophasiques. Leurs propriétés sont données dans les tableaux 2 et 3. Les pigments 1 à 6 sont très labiles dans l'air. Le stockage, les chromatographies et les divers traitements sont toujours réalisés dans une atmosphère d'azote.

Les pigments 1, 2 et 3 sont très solubles dans le méthanol, l'éthanol, le chloroforme, l'éther, le n-hexane, l'éther de pétrole et le sulfure de carbone. La couleur de ces solutions est toujours jaune sauf les solutions de 1 et 2 dans le sulfure de carbone qui sont roses. Le pigment 4 est très soluble dans le chloroforme, l'éther, le n-hexane et peu soluble dans l'éthanol. Ces solutions sont jaune-orange. Les pigments 5 et 6 sont solubles dans l'éther de pétrole, le n-hexane et le chloroforme. Ils sont très vite détruits par l'air. Le pigment 7 est insoluble dans l'éther de pétrole et le n-hexane, peu soluble dans l'acétone, l'éther, le benzène, le sulfure de carbone et la pyridine, très soluble dans l'éthanol, le méthanol et le chloroforme.

PLANCHE IV

Quelques aspects ultrastructuraux des « granules » de la fraction 5.

Fig. 1 : × 60.000	Fig. 4 : × 49.000
Fig. 2 : × 68.000	Fig. 5 : × 44.000
Fig. 3 : × 23.000	Fig. 6 : × 30.000

PLANCHE V

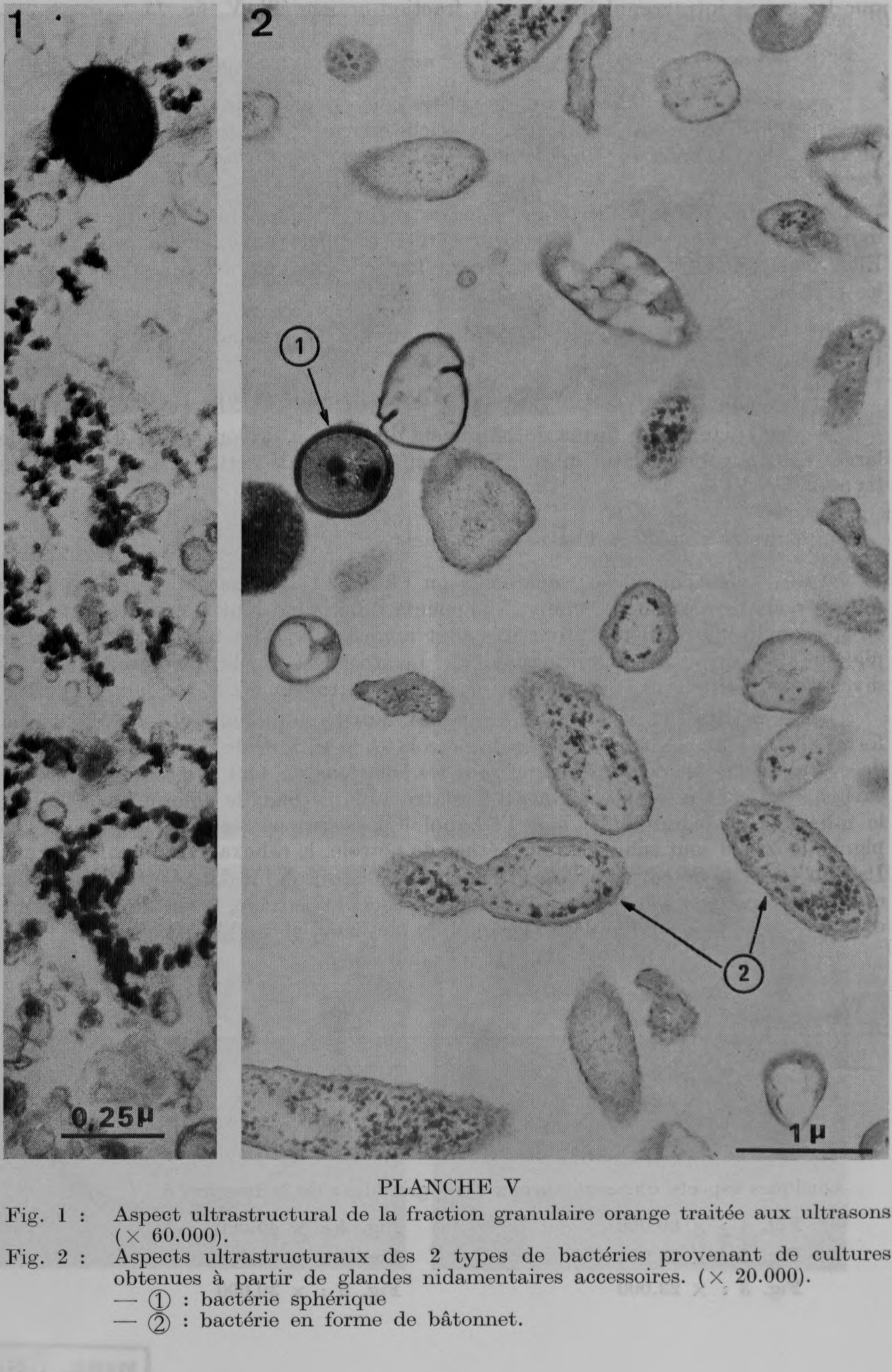


PLANCHE V

Fig. 1 : Aspect ultrastructural de la fraction granulaire orange traitée aux ultrasons (× 60.000).

Fig. 2 : Aspects ultrastructuraux des 2 types de bactéries provenant de cultures obtenues à partir de glandes nidamentaires accessoires. (× 20.000).
— ① : bactérie sphérique
— ② : bactérie en forme de bâtonnet.

TABLEAU II

Identification biochimique des pigments extraits des glandes nidamentaires accessoires de seiche

Pigment	Abondance relative	Rf 1	Rf 2	Couleur	Réaction Carr-Price	Réaction H_2SO_4	Coefficient de répartition
Épiphase							
Pigment 1	5 %	0.79	0.98	jaune	+	+	100 : 0
Pigment 2	2 %	0.71	0.98	jaune	+	+	100 : 0
Pigment 3	2 %	0.64	0.98	orange-jaune	+	+	—
Pigment 4	8 %	0	0.98	jaune-orange	+	+	—
Hypophase							
Pigment 5	5 %	0	0.95	orange	+	+	—
Pigment 6	16 %	0	0.90	jaune	+	+	—
Pigment 7	48 %	0	0.81	orange-rouge	+	+	0 : 100

DISCUSSION

Les glandes nidamentaires accessoires de la seiche sont en activité sécrétoire bien avant que les couleurs n'y apparaissent. On constate qu'il y a ensuite corrélation entre, l'évolution génitale, la coloration des glandes et le nombre de bactéries symbiotiques occupant les lumières des tubules glandulaires.

Cependant dans la masse glandulaire, les tubules ne sont pas toujours d'une même teinte ; on peut se demander s'il existe plusieurs types de colorants ou de bactéries colorées ou encore s'il y a plusieurs étapes de coloration d'un ou plusieurs types de bactéries intra-glandulaires. Les différentes couleurs observées *in situ* se retrouvent dans les fractions isolées des gradients de densité.

En fait, l'homogénat de la glande extrait avec un mélange de chloroforme-méthanol (1/1), contient 7 pigments. Après une répartition de ces pigments dans l'éther de pétrole et le méthanol à 90 %, quatre pigments (pigments 1 à 4 formant 17 % de l'extrait original) apparaissent dans l'épiphase. Les autres pigments (pigments 5 à 7) formant 60 % de l'extrait original, sont trouvés dans l'hypophase.

Le pigment 1 a toutes les propriétés du béta-carotène. Une chromatographie sur une couche mince de $CaCO_3/MgO/Ca(OH)_2$ éluée dans le mélange benzène/chloroforme/acétone (50/40/50) ne montre qu'une fraction correspondant avec le béta-carotène (Hager et coll., 1966) et la cochromatographie du pigment 1 et de béta-carotène du commerce (Merck) ne donne aucune séparation.

Les pigments 2 à 6 sont probablement des caroténoides : l'identification en cours est très difficile.

Quant au pigment 7, qui est le pigment le plus important de la glande, il n'est pas soluble dans l'éther de pétrole, ni dans le n-hexane, légèrement soluble dans l'acétone, l'éther, le benzène, le sulfure de carbone et la pyridine, mais très soluble dans l'éthanol, le méthanol et le chloroforme. En outre le spectre d'absorption et les propriétés chromatographiques montrent qu'il s'agit d'un caroténoide de nature polaire correspondant avec la SEPIAXANTHINE (Decleir et Richard, 1972).

TABLEAU III

Propriétés et caractéristiques spectrales des pigments extraits des glandes nidamentaires accessoires de la seiche

Pigment	Maxima d'absorption (nm)						
	Chloroforme	Ether	*n*-Hexane	Ether de pétrole	Méthanol	Ethanol	CS_2
Épiphase							
Pigment 1	436/461/485	438/450	426/448/475	422/445/472	427/447/472	426/449/473	450/485/510
Pigment 2	—	450/460	434/454/480	432/454/480	435/452/478	—	490
Pigment 3	—	410/420/443	436/459/492	400/424/447	462/495	—	—
Pigment 4	406/431/452/475	410/420/442	399/425/446/467	—	399/425/445	397/423/444/468	—
Hypophase							
Pigment 5	434/456/481	—	—	—	—	—	—
Pigment 6	434/458/487	—	—	—	—	—	—
Pigment 7	458/481/516	445/472/502	insoluble	insoluble	445/470/501	448/472/503	475/500/534

Les granules colorés, isolés des lumières des tubules glandulaires sont très hétérogènes et difficiles à bien séparer dans un gradient de densité. Les types les plus fréquents ont tous cependant des caractéristiques particulières qui permettent de les identifier à des bactéries :

— les dimensions varient entre 0,5 et 1 μ

— les figures de division sont fréquemment observées (Pl. III, fig. 1 et 3)

— les parois sont épaisses et présentent souvent des aspects « chevelus » typiques des bactéries.

Cela montre qu'il y a identité entre teintes de la glande et types de bactéries. Cette observation confirme les observations de Bloodgood (1977) obtenues chez le calmar *Loligo pealii*.

Le pigment « corail » semble bien lié à une sous-fraction granulaire intrabactérienne d'un type de bactérie symbiotique de la glande qui serait donc le site de la SEPIAXANTHINE.

En culture, on obtient cependant des colonies blanchâtres et brunâtres. On y retrouve pourtant deux types de bactéries identifiés dans les tubules glandulaires. Ceux-ci ne montrent donc pas de coloration caractéristique. D'autre part, l'autofluorescence dans le rouge que nous avons pu observer *in situ* dans la glande, n'a pu être visualisée à partir de ces cultures bactériennes.

La sécrétion glandulaire exocrine permettrait donc la multiplication, la croissance et la différenciation de quelques types bactériens. La pauvreté du milieu de culture artificiel peut expliquer que l'on ne retrouve pas *in vitro* la totalité des caractères spécifiques des bactéries. L'élaboration intrabactérienne du pigment 7, orange, dont l'abondance suit l'évolution sexuelle de la seiche serait donc liée aux sécrétions endocrines contrôlant la maturation génitale. On sait en effet par des expériences d'élevages en photopériodes contrôlées, qu'il y a corrélation entre l'état sexuel et la couleur des glandes, ce, sans relation avec la taille de l'animal, ou sa nourriture (Richard, 1967). Les sécrétions exocrines des glandes nidamentaires accessoires pourraient se modifier sous l'action des hormones gonadotropes des glandes optiques (Richard, 1971) et induire des transformations pigmentaires dans des bactéries symbiotiques ou encore favoriser le développement de bactéries pigmentées.

La question qui se pose est de préciser la signification physiologique de cette élaboration des pigments dont la SEPIAXANTHINE représente la fraction la plus importante. Les œufs de seiche ne contiennent pas, ou très peu de caroténoides. Une extraction des œufs avec l'acétone ou avec le chloroforme-méthanol (1/1) même après passage aux ultrasons ne révèle aucune extraction de pigment. Une saponification directe des œufs avec le mélange KOH à 60 % - éthanol (1/10) suivie de lavage avec un mélange d'eau et d'éther fait apparaître tout le pigment de couleur jaune-orange dans la phase aqueuse. Ce pigment est soluble dans un tampon phosphate (pH = 7,7), dans le chloroforme et le méthanol, mais est insoluble dans l'éther, le benzène, la pyridine, le sulfure de carbone, le n-hexane et l'acétone. Le spectre dans le tampon phosphate a un maximum à 290 nm et le spectre dans le méthanol ou le chloroforme ne montre aucun maximum. Il ne s'agit donc pas d'un caroténoide. En outre le pigment ne montre pas de changement de couleur après réduction avec le borohydrure de sodium ($NaBH_4$) ou le thiosulfate de sodium (Van den Branden et Decleir, 1976). Il ne s'agit également pas d'un ommochrome.

L'élaboration de ces pigments dans la glande nidamentaire accessoire résulte bien d'un mécanisme métabolique lié à la transformation d'une sécrétion par des bactéries symbiotiques de la glande. On peut se demander si ces bactéries sont spécifiques. On sait en effet que Zirpolo (in Pierantoni) cite *Bacillus sepiae n. sp.* comme une bactérie symbiotique spécifique des glandes nidamentaires de la seiche. Dans ce cas, comment se réalise la symbiose chez la seiche? Une première hypothèse serait de penser à une contamination *in ovo*. On sait que les sécrétions des glandes nidamentaires principales situées sous les glandes nidamentaires accessoires (Pl. I) forment les enveloppes ovocytaires. Etant donné la proximité des orifices sécrétoires de ces deux types de glandes nidamentaires. il n'est pas exclu que quelques bactéries soient entraînées avec les produits de sécrétion et puissent assurer chez la seiche à l'éclosion, une contamination. Cependant, il faudrait considérer que ces bactéries souches survivent, en attendant que les sécrétions des glandes nidamentaires accessoires leur permettent de se développer ! On doit exclure des présomptions, la contamination de jeunes seiches par des bactéries provenant d'adultes ; en effet, en élevage, les pontes sont isolées avant l'éclosion : les jeunes seiches ne sont donc jamais en contact avec d'autres animaux.

Une autre hypothèse que devraient confirmer des identifications et des inoculations de bactéries, serait de considérer que c'est la sécrétion glandulaire qui est spécifique et qui induit cette élaboration de pigments caroténoides dans des souches de bactéries banales. Le rôle de la glande nidamentaire accessoire pose alors un problème biologique. Comme la corrélation entre concentration de SEPIAXANTHINE et maturité des femelles est évidente, on peut se demander si cette sécrétion ne joue pas un rôle attractif vis-à-vis des mâles. La distribution par couple des seiches n'est en effet permanente qu'au moment de la ponte (Richard, 1971). Elle pourrait s'expliquer par la conjonction d'émission de la sécrétion des glandes nidamentaires accessoires et de la formation de coques ovocytaires.

A côté d'un rôle d'excrétion de phéromones déjà proposé (Decleir et Richard, 1972) il est plausible de supposer un rôle de bioluminescence. En effet, les mâles des céphalopodes sont attirés par la lumière. Une bioluminescence a souvent été décrite chez divers céphalopodes (Berry, 1920 ; Okada, 1927 ; Herring, 1977). Nous avons regardé des glandes et des extraits de glandes dans l'obscurité mais nous n'avons jamais pu constater de bioluminescence. Cette hypothèse n'est probable que si la combinaison luciférine-luciférase se réalise dans la glande ou dans les bactéries, selon un mécanisme que nous ne comprenons pas encore. Il se peut, si une telle bioluminescence existe, qu'elle se réalise dans une bande spectrale que l'œil humain ne décèle pas. Les recherches en ce domaine ne sont pas suffisamment avancées pour nous permettre d'accréditer une telle hypothèse.

REMERCIEMENTS

Nous voulons remercier Hugo De Coninck pour son aide très efficace dans cette recherche. Nous voulons exprimer aussi notre gratitude envers Madame Françoise Bonet, technicienne au LA 148 de l'Université de Lille I et le Professeur De Groodt-Lasseel et son laboratoire d'histologie (Université d'Anvers - R.U.C.A.) où a été réalisée une partie des études au microscope électronique.

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Annales Soc. r. Zool. Belg. — T. 108 (1978) — fasc. 3-4 — pp. 141-149 — Bruxelles 1979

Juillet 1979 (*Communication reçue le 16 décembre 1978*)

TENUIPTERIA GEULEMENSIS (MOLLUSCA : BIVALVIA), AN INOCERAMID SPECIES FROM THE UPPER MAASTRICHTIAN OF THE SINT PIETERSBERG AREA, THE NETHERLANDS

by

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ABSTRACT

The inoceramid species *Tenuipteria geulemensis* (F. Vogel, 1895) is recorded for the first time from the Upper Maastrichtian (*Belemnella junior* and *B. casimirovensis* Zones) in the Maastrichtian type area (Sint Pietersberg, Maastricht, The Netherlands). It can be used as an index fossil for the Upper Maastrichtian in northern and eastern Europe, and is very similar to the North American Maastrichtian species *T. argentea* (Conrad).

RÉSUMÉ

Tenuipteria geulemensis (F. Vogel, 1895) est une espèce d'inocérame non encore signalée dans le Maastrichtien supérieur (zone à *Belemnella junior* et zone à *B. casimirovensis*) de la région type de l'étage (Montagne Saint Pierre près de Maastricht, Pays-Bas). Elle peut être employée comme fossile guide dans les dépôts du Maastrichtien supérieur d'Europe du Nord et de l'Est ; elle est très proche de l'espèce maastrichtienne nordaméricaine *T. argentea* (Conrad).

ACKNOWLEDGMENTS

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INTRODUCTION

The Maastrichtian, uppermost stage of the Cretaceous has yielded in its type area a very rich fauna known at least since the 18th century.

Part of a paper presented at the meeting of December 16, 1978 ; published with the permission of the Director of the K.B.I.N., Brussels.

The fauna from the Maastrichtian type area — the Sint Pietersberg — was listed by J. Bosquet (1860). Since then no-one has attempted so comprehensive a task, but many groups have been monographically studied (e.g. Ammonites, A. de Grossouvre [1908] ; Gastropods, F. Kaunhowen [1897] ; Foraminifera, B. J. Romein [1962] and J. Hofker [1966] ; Echinoids, J. Lambert [1911], J. Smiser [1935], M. Meijer [1965] ; Ostracods, G. Deroo [1966] ; Bryozoans, E. Voigt [1953] ; « Calcisphaerulidae », J. M. Villain [1975]). The Bivalves were studied by F. Vogel (1895), who based his work on the collections of the universities at Bonn (G.F.R.), Leiden (The Netherlands) and Liège (Belgium). Later work has been published on the Rudists (W. A. E. Van de Geijn, 1940) and on the Pectinids (A. V. Dhondt, 1971, 1972a, b, 1973a, b, 1976). I have lately undertaken the study of the other Pteriomorphia from the Maastrichtian type area ; these include an « inoceramid » species from the Maastrichtian « tufkrijt » (= Maastrichtien sensu Dumont, 1849 = Maastricht Formation of W. M. Felder, 1975).

In Bosquet's list no *Inoceramus* species is listed as occurring in the « Maastrichtsch Krijt » (= Maastricht Formation), or the Upper Maastrichtian in the international sense (Zone of *Belemnella junior* and Zone of *B. casimirovensis*).

I have mainly studied the material from the collections of the K.B.I.N. - I.R.Sc.N.B. : the « old » collections : Bosquet, Ubaghs, Nyst, Cornet, etc., collections more recently acquired such as the M. Meijer collection, and the vast amount of material collected by bulk sampling along and in the Albert Canal in the 1930's under M. Glibert and in 1955 under L. Van de Poel. Among this material (at a rough estimate Pteriomorphs number at least 75.000 specimens) is one species not previously cited from the Maastrichtian type area ; this is a « borderline » inoceramid, *Tenuipteria geulemensis* (F. Vogel, 1895), recorded under different names from the Upper Maastrichtian in most northern and eastern European deposits of the temperate realm.

CLASSIS BIVALVIA

Subclassis Pteriomorphia
Superfamilia Pteriacea
Familia *Inoceramidae*

Tenuipteria Stephenson, 1955
(emended diagnosis in I. G. Speden, 1970, p. 23)

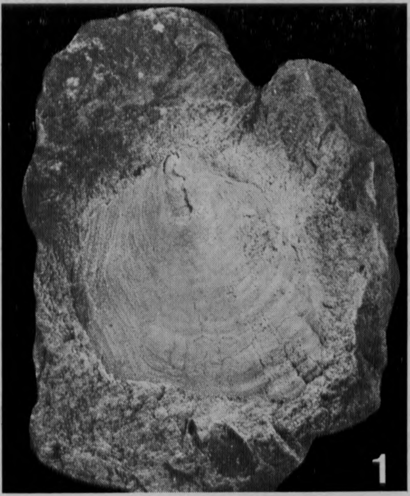
Tenuipteria geulemensis (F. Vogel, 1895)

. 1895 *Avicula Geulemensis* nov. sp. — F. Vogel, pp. 28-29, pl. 2, figs. 3-6 ;
. 1902 *Avicula* spec. — J. P. J. Ravn, p. 81, pl. 1, figs. 4-5 ;

PLATE I

Fig. 1 : right valve, × 2, Kunrader Limestone, Kunrade, Zuid-Limburg (T.C.M.I. 10165) ;
Fig. 2 : double steinkern, right valve on top, × 1.25, Maastrichts Tufkrijt, Sint Pietersberg, Maastricht, Coll. Bosquet (T.C.M.I. 10166) ;
Fig. 3 : right valve, × 1, Kunrader Limestone, Kunrade, Zuid-Limburg (T.C.M.I. 10167) ;
Fig. 4 : left valve, × 1, *B. junior* Zone, Hemmoor, Schleswig-Holstein, G.F.R. (Niedersächsisches Landesamt für Bodenforschung) ;
Fig. 5 : interior of right valve, × 1, Maastrichts Tufkrijt ; Sint Pietersberg, Maastricht, Coll. Bosquet (T.C.M.I. 10168) ;
Fig. 6 : interior of right valve, × 2, Maastrichts Tufkrijt, Sint Pietersberg, Maastricht, Coll. Bosquet (T.C.M.I. 10169).

PLATE I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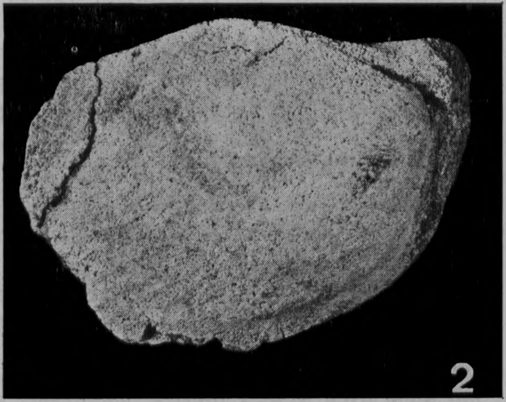
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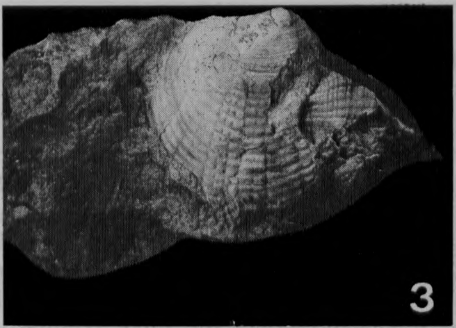
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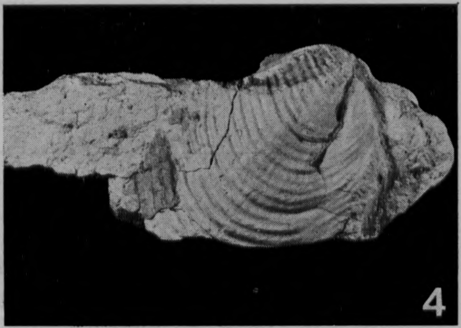
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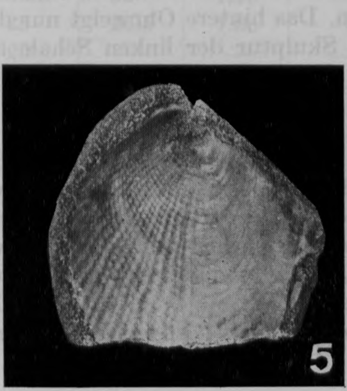
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6

p.p. 1922 *Inoceramus tegulatus* — H. ØDUM, pp. 1-13, figs. 1, 2, 3, 7 ;
. 1959 *Inoceramus tegulatus* — S. A. DOBROV and M. M. PAVLOVA, pp. 150-151, pl. 23, figs. 1-4 ;
1959 « *Inoceramus tegulatus* » Ødum — O. SEITZ, p. 124 ;
. 1965 *Inoceramus dobrovi* n. sp. — J. A. JELETZKY, pp. 955-956 ;
1969 *Spyridoceramus tegulatus* — L. R. COX in MOORE, p. N 320, figs. C 48 3a-b ;
. 1970 *Tenuipteria dobrovi* — I. G. SPEDEN, p. 34, pl. 2, figs. 4-6.

non 1842 *Inoceramus tegulatus* F. von HAGENOW, nec 1922 *I. tegulatus* H. ØDUM, figs. 4, 5, 6, nec 1932 *I. tegulatus* D. WOLANSKY, nec 1956 *I. tegulatus* O. SEITZ, p. 4, nec 1961 *I. tegulatus* O. SEITZ, pp. 123-124, nec 1965 *I. tegulatus* J. A. JELETZKY, p. 955, nec 1968 *I. tegulatus* S. P. KOTSYUBINSKI, p. 148, pl. 28, fig. 3, pl. 29, fig. 8, nec 1970 *Tenuipteria tegulata* I. G. SPEDEN, pp. 6-8, pl. 2, figs. 1, 2, 3.

Type specimen :

As lectotype I chose the specimen figured in F. VOGEL, pl. II, fig. 4, in the Rijksmuseum voor Geologie in Leiden (The Netherlands).

Type locality :

« Geulem » (Geulhem in modern spelling, Limburg, The Netherlands).

Geological Horizon :

« Obere Mucronatenkreide » (in Geulhem : Mc-Md of UHLENBROECK, 1912, Upper Maastricht Formation of FELDER, 1975).

Original description (VOGEL, 1895, p. 28)

Von dieser Muschel ist meistens die äussere Schalschicht erhalten ; dieselbe liegt jedoch dem Gestein so fest auf, dass sie kaum abzulösen ist. Die Steinkerne, welche sich mehrfach finden, geben nur ein undeutliches Bild der Muschel, da die Ohren stets abgebrochen sind, und sie dadurch das Aussehen einer *Pholadomya* erhalten. Nur wo eine isolierte Klappe einen Steinkern hinterliess, ist dieser vollständig. Die Schale ist ungleichseitig und ungleichklappig ; die linke Klappe ist stark gewölbt, mit weit überragendem Wirbel, die rechte nur schwach gewölbt ; vorn ein kleines, hinten ein sehr grosses und breites Ohr. Der grade Schlossrand bildet mit dem ebenfalls graden Vorderrand einen beinah rechten und mit dem gebogenen Hinterrand einen stumpfen Winkel. Der Stirnrand ist gebogen.

Der Mittelteil der Schale ist geziert mit etwa 20 flachen und breiten, radialen Rippen, welche von concentrischen gekreuzt werden. Das hintere Ohr zeigt nur die concentrischen Rippen und radiale Streifung. Die Skulptur der linken Schale ist weniger kräftig als die der rechten.

Translation of the original description :

Only the external shell layer of this bivalve is preserved ; it is so strongly attached to the sediment that it cannot be loosened. Internal moulds are numerous but give an incomplete impression of the bivalve, because the ears are always broken off and thus the specimen looks like a *Pholadomya*. Only when an isolated valve has become a Steinkern will this be complete. The shell is inequilateral and inequivalve ; the left valve is very inflated with a strongly projecting umbo and weakly inflated right valve. At the anterior side is a small ear ; at the posterior side a very large and wide ear. The straight dorsal margin forms with the straight anterior margin an almost right angle, and an obtuse angle with the rounded posterior margin. The pallial margin is rounded.

The central part of the shell is ornamented with 20 flattened, wide plicae, crossed by concentric folds. The posterior auricle bears only concentric ribs and radial striation. The ornamentation of the left valve is not so pronounced as that of the right valve.

Additional description :

Material studied :

Geulhem : 2 steinkerns of left valves, 2 steinkerns of right valves, 1 left and 1 right valve with shell material ;

Sint Pietersberg : 5 steinkerns of left valves, 5 steinkerns of right valves, 1 left and 4 right valves with shell material ;

Kunrade : 2 steinkerns of double valves specimens, 3 right valves with shell material ;

Houthalen (in coal pits) : 2 incomplete left valves with shell material.

Measurements (in mm.)

1. U.P.D.	2. W.	Ratio 1/2	3. dorsal margin	Ratio 1/3	4. plicae	5. side	locality
87	74.4	1.29	54	1.61	18	L	Geulhem
63	48	1.31	37.4	1.68	—	L	»
52.4	39.7	1.32	27.2	1.32	—	L	»
45.3	37.2	1.22	23.4	1.22	—	L	»
29.4	27.2	1.08	16.4	1.67	19	R	»
41.2	33	1.24	18.6	2.22	—	L	Sint Pietersberg
37.2	34.8	1.07	—	—	22	R	»
52.2	36	1.45	26.2	1.99	—	L	»
46.3	35.4	1.30	20	2.32	—	R	»
45.8	35.4	1.29	24.0	1.91	—	L	»
40.5	35	1.16	—	—	—	R	»
28	26.5	1.06	—	—	18	L	» Md
20	—	—	—	—	17	L	» Mc
27.4	22.4	1.25	17.6	1.56	—	R	»
38.2	31.7	1.21	27.8	1.37	24	R	»
39.6	—	—	—	—	26	R	»
31	—	—	—	—	19	R	»
20	—	—	—	—	17	L	»
42.2	35.4	1.19	22	1.92	27	R	Kunrade
24.8	—	—	14.8	1.68	—	R	»
16.2	—	—	—	—	—	R	»
27	—	—	—	—	21	R	»
28.2	—	—	—	—	22	R	»

Abbreviations used :

U.P.D. : umbo-pallial diameter : distance from the umbo to the pallial margin, perpendicular to the dorsal margin ;

W. : the longest distance from the anterior to the posterior side of the disc perpendicular to its U.P.D. ;

P.D.M. : posterior dorsal margin : distance from the umbo to the end of the margin at the dorsal extension of the disc ;

L : left ; R : right.

DESCRIPTION

Inequivalve, medium-sized (U.P.D. 16-90 mm, n = 23) species with inequilateral valves with prosogyrate umbones.

Right valve : rarely flattened, generally moderately inflated, the umbo projecting (2 to 4 mm) above the dorsal (= hinge) margin ; anterior auricle triangular and small (auricle Hmax = 6 mm, W = 5.5 mm on a specimen with U.P.D. = 42.2 mm) ; posterior extension of the valve broad ; W. varies from 22.4 mm to 35.4 mm (n = 7), U.P.D./W. varies from 1.07 to 1.30.

Left valve : inflated, with a wide projecting umbo (5 to 9 mm) above the dorsal margin ; anterior auricle as on the right valve ; W. varies from 26.5 to 74.4 mm (n = 8), U.P.D./W. varies from 1.06 to 1.45 ; postero-dorsal margin straight, 14.8 to 54 mm (n = 13) long, U.P.D./P.D.M. varies from 1.37 to 2.32.

The available material suggests that right valves are somewhat smaller than left valves : average U.P.D./W. for right valves is 1.18, whereas for left valves it is 1.27.

Both valves are covered with the same ornamentation : a combination of radial and concentric plicae which seems to be slightly more pronounced on right than on left valves ; on some specimens the radial plicae are of equal development, but on others, each alternating interspace is somewhat deeper ; where concentric and radial plication are of similar strength the sculpture seems to consist of small juxtaposed squares separated by narrow radial and concentric furrows.

Right valves :

Number of plicae counted at the ventral margin :

plicae :	19	19	21	22	22	24	26	27
U.P.D. in mm	29.4	31	27	28.2	37.2	38.2	39.6	42.2

The radial plication does not cover the complete shell ; on the posterior part of the valve only one-third to two-fifths bears concentric ornamentation ; at the anterior side, the radial plication reaches the side margin. Three right valves (from Kunrade) have a more pronounced concentric than radial ornamentation and two only a slight radial plication.

Left valves :

Number of plicae counted at the ventral margin :

plicae :	17	18	19
U.P.D. in mm :	20	28	90

Only one of the valves shows a well developed plication and it seems to cover the whole valve ; it reaches the anterior margin and it almost reaches the posterior margin.

COMPARISON AND SYNONYMY

The description and figures given by F. VOGEL for « *Avicula geulemensis* » are perfectly adequate, but have been totally ignored by later authors. The species was not recognised as an inoceramid by VOGEL because of the very thin, incomplete shell and because of the total absence of ligamental areas on the specimens he studied. The general shape and the ornamentation of the specimens from Limburg are identical with the material described and figured by H. ØDUM, 1922 (figs. 1, 2 3, 7 non figs. 4, 5, 6) ; the Danish specimens were proved by I. G. SPEDEN 1970 to be identical with those described as *Inoceramus tegulatus* by S. A. DOBROV and M. M. PAVLOVA, 1959 and for which J. A. JELETZKY created the name *Inoceramus dobrovi*. JELETZKY's name thus becomes a junior subjective synonym of « *Inoceramus* » *geulemensis* (VOGEL). L. R. COX in MOORE, 1969 used the name of the Lower Maastrichtian species (= *Inoceramus tegulatus* F. von HAGENOW, 1842) from Rügen, but copied ØDUM's description and those of his figures which apply to the Upper Maastrichtian inequivalve species.

I. G. SPEDEN, 1970 gave a detailed discussion of the inoceramid species belonging to the genus *Tenuipteria* from N. America and Europe, and clearly stated the differences between *T. tegulata* (von HAGENOW) and *T. dobrovi* (JELETZKY) (= *T. geulemensis*). The *Tenuipteria* group has a wider geographical distribution than stated by I. G. SPEDEN. M. A. PERGAMENT, 1974 (pp. 192-193, pl. 45, figs. 5, 6, pl. 46, fig. 1) described *Inoceramus kusiroensis* NAGAO et MATSUMOTO, 1940 from the Maastrichtian of Kamchatka and Japan and stated this species to be close to « *Inoceramus tegulatus* s.l. ».

Among the specimens of *Tenuipteria geulemensis* from Limburg is one left valve with an almost complete hinge : the specimen is unfortunately not well enough preserved to be figured but is very close to pl. 3, fig. 3 of I. G. SPEDEN (*T. argentea* [Conrad]). Without seeing specimens of *T. argentea* I cannot decide on whether *T. geulemensis* and *T. argentea* are synonymous ; the ornamentation, the general shape, the hinge appear almost identical but the measurements seem to be different ; this could be due to the methods used, but at present no conclusion can be drawn.

Biogeographical and stratigraphical distribution :

Restricted to the Upper Maastrichtian (*B. junior* Zone and *B. casimirovensis* Zone) of Limburg (Belgium and the Netherlands), Hemmoor (Schleswig-Holstein, G.F.R. — only *B. junior* Zone), Denmark (ØDUM, 1922, SPEDEN, 1970 — Upper Maastrichtian), Caucasus and Crimea (DOBROV and PAVLOVA, 1959 and personal communication of M. A. PERGAMENT, April 1978 — Upper Maastrichtian).

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MORFOLOGISCHE GEGEVENS BETREFFENDE « *RANA ESCULENTA* » IN BELGIË (ANURA, RANIDAE)

(Morphological data concerning « *Rana esculenta* » in Belgium) (Anura, Ranidae)

door

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SAMENVATTING

124 groene kikkers, verspreid over gans België, werden onderzocht naar de vorm van de metatarsale knobbel en naar de verhoudingen lengte tibia/lengte metatarsale knobbel en lengte teen 1/lengte metatarsale knobbel.

Alhoewel geen duidelijke groepen-onderverdeling optreedt, kunnen een aantal individuen, naar de criteria van Berger en van Günther, als vermoedelijk *R. lessonae* bestempeld worden. Het overgrote deel lijkt echter « *esculenta* » of intermediair te zijn. Eén jong individu vertoont de verhoudingen van « *ridibunda* ». Verder onderzoek op vers en levend materiaal is evenwel vereist om deze gegevens te bevestigen.

SUMMARY

The form of the metatarsal tubercle and the ratio's : length of tibia/length of metatarsal tubercle and length of toe 1/length of metatarsal tubercle were analysed on 124 green frogs, distributed throughout Belgium.

Although no discrimination into clear-cut groups could be observed, using the criteria of Berger and of Günther, some individuals can be considered as « *R. lessonae* », but the major part seems to be « *esculenta* » or intermediate. One young specimen shows the biometrical characters of « *ridibunda* ». More investigations on fresh or living specimens are needed to corroborate these results.

1. INLEIDING

Naar aanleiding van de onderzoekingen van Berger (1966, 1973) op Poolse « groene kikker »-populaties, zijn de laatste jaren in Polen, Duitsland en Zwitserland talrijke studies op « *Rana esculenta* » gebeurd.

Uit al deze studies blijkt dat *Rana esculenta* een hybriede zou zijn, ontstaan uit twee oudervormen, vroeger beschreven als *R. lessonae* Camerano en *Rana ridibunda* Pallas. Dit wordt gestaafd door morfologische, ecologische, histologische, caryologische en serologische kenmerken (Berger, *op. cit.*; Günther, 1968, 1970, 1973; Tunner, 1970, 1972, 1973, 1974; Blankenhorn, et al., 1971, 1973a, 1973b).

Volgens de laatste onderzoekingen zouden populaties van « *esculenta* » bestaan uit twee soorten diploïden, waarvan de ene samenleeft met *lessonae*, de andere met *ridibunda*, en twee soorten triploïden, waarvan de ene twee chromosomenstellen *ridibunda* en één stel *lessonae* zou bezitten en de andere omgekeerd (Uzzell, 1975).

De morfologische verschillen berusten op kleur- en vlekkenpatroon van rug en achterpoten en vooral op de lengte van tibia, teen-1 lengte en de lengte van de binnenste metatarsale knobbel (cfr. Berger, 1973; Günther, 1973). Vooral de verhoudingen « teen 1-lengte/lengte metatarsale knobbel » en « tibia-lengte/lengte metatarsale knobbel » laten een vrij goede scheiding tussen de drie vormen toe.

Over het voorkomen van deze drie vormen in België zijn, naar mijn weten, geen betrouwbare gegevens voorhanden.

In Nederland meent Hoogmoed (1975) wel twee exemplaren van *ridibunda* te kunnen aantonen (één uit Leiden en één uit Surhuisterveen (Friesland). Ook in het Saar-Moesel gebied konden naar bovenstaande criteria, *esculenta* en *lessonae* aangetoond worden (Halfmann & Müller, 1972).

Het is dus te verwachten dat ook in België meerdere vormen zouden kunnen bestaan. Daartoe onderzochten wij alle beschikbare *R. esculenta* uit de kollekties van het K.B.I.N.W. te Brussel en van het R.U.C.A. te Antwerpen.

Ik dank hierbij de Hr. G.-F. de Witte (Brussel) en Prof. Dr. W. N. Verheyen (Antwerpen) voor het ter beschikking stellen van dit materiaal.

2. RESULTATEN

2.1. *Materiaal en methode*

In totaal werden 124 exemplaren *Rana esculenta* onderzocht, afkomstig uit gans België (zie tabel 2). Het betreft hier dus geen streng gelokaliseerde populaties, maar at random gekollekteerd en gefixeerd museum-materiaal.

Daarom werden alleen volgende kenmerken nagegaan : romplengte, tibialengte, metatarsale knobbellengte, teen-1-lengte en vorm van metatarsale knobbel.

Andere morfologische kenmerken, zoals vlekkenpatroon, kunnen op museummateriaal moeilijk beoordeeld worden. Ook moet rekening gehouden worden met het feit dat de maten genomen werden op gefixeerd materiaal, wat waarschijnlijk, tengevolge van inkrimping, invloed heeft op de absolute afmetingen en met het feit dat, ondanks alle voorzorgen, twee onderzoekers niet noodzakelijkerwijze op dezelfde wijze meten. Voorzichtigheid is dus geboden bij het vergelijken van onze resultaten met die van andere onderzoekers.

2.2. *Vorm van de metatarsale knobbel*

De vorm van de metatarsale knobbel is niet altijd gemakkelijk te beoordelen, te meer daar er zeer veel intermediaire vormen bestaan (cfr. Berger 1966 fig. 3,).

Tabel 1 geeft een samenvatting van het aantal individuen dat naar metatarsale knobbelvorm tot de een of andere vorm gerekend werd (vertikaal) en in welk vooropgesteld gebied deze individuen volgens de grafiek (Tel/TC)/(Tib/TC) (fig. 1) bleken te vallen (horizontaal).

Uit deze tabel blijkt dat verreweg het grootste aantal individuen, naar de vormcriteria van Berger, als « *esculenta* » kunnen gekenmerkt worden, maar dat ze volgens de verhouding der relatieve afmetingen (fig. 1) bijna egaal over de grafiek verspreid liggen.

Diegenen die min of meer duidelijk als *lessonae* herkend worden, liggen ook in

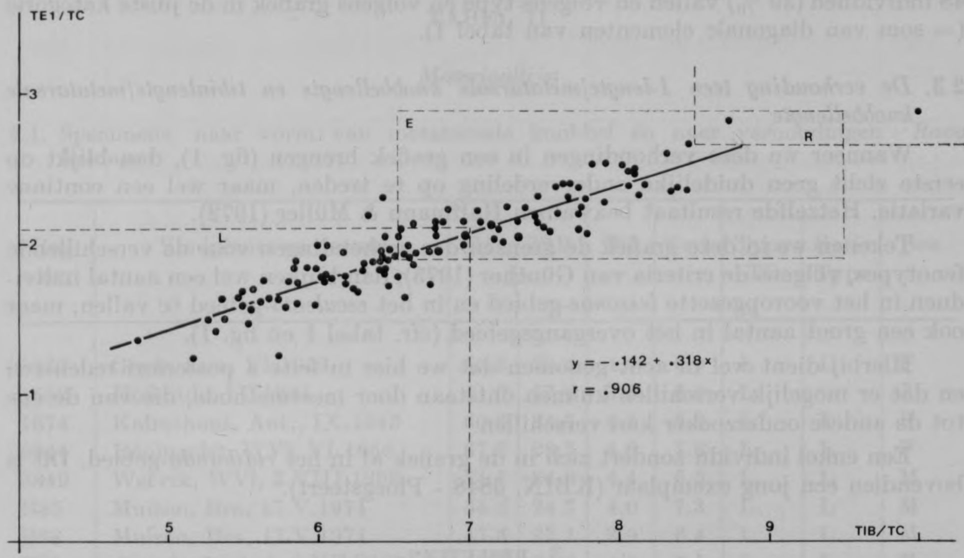

Fig. 1. — Grafiek der verhoudingen teen 1 lengte/metatarsale knobbellengte t.o.v. tibialengte/metatarsale knobbellengte bij « *Rana esculenta* » in België.
L = *lessonae;* E = *esculenta;* R = *ridibunda,* volgens de kriteria van Günther.

TABEL I

Rangschikking der « esculenta » *individuen naar metatarsale knobbelvorm (vertikaal) en volgens de grafiek (Te1/TC)/(Tib/TC) (cfr. fig. 1)*

L = *lessonae,* E = *esculenta,* R = *ridibunda,* LE = intermediair *lessonae-esculenta,* ER = intermediair *esculenta-ridibunda.*

type TC	volgens grafiek				
	L	E	LE	R	Som
L	9	0	0	0	9
E	23	25	29	0	78
LE	10	3	13	0	26
ER	0	10	0	0	10
R	0	0	0	1	1
Som	42	38	42	1	124

de grafiek in het vooropgestelde *lessonae*-gebied. Hetzelfde geldt voor het enige als *ridibunda* gekenmerkte individu.

Het is dus wel duidelijk dat, naar de vorm van de metatarsale knobbel alleen, moeilijk een betrouwbare determinatie van museummateriaal kan gebeuren. Slechts

48 individuen (39 %) vallen én volgens type én volgens grafiek in de juiste kategorie (= som van diagonale elementen van tabel I).

2.3. *De verhouding teen 1-lengte/metatarsale knobbellengte en tibialengte/metatarsale knobbellengte*

Wanneer we deze verhoudingen in een grafiek brengen (fig. 1), dan blijkt op eerste zicht geen duidelijke onderverdeling op te treden, maar wel een continue variatie. Hetzelfde resultaat bekwamen Halfmann & Müller (1972).

Tekenen we in deze grafiek de grenzen der verhoudingen voor de verschillende fenotypes, volgens de criteria van Günther (1973), dan blijken wel een aantal individuen in het vooropgezette *lessonae*-gebied en in het *esculenta*-gebied te vallen, maar ook een groot aantal in het overgangsgebied (cfr. tabel 1 en fig. 1).

Hierbij dient wel in acht genomen dat we hier in feite a posteriori redeneren en dat er mogelijk verschillen kunnen ontstaan door meetmethode, die van de ene tot de andere onderzoeker kan verschillen.

Een enkel individu zondert zich in de grafiek af in het *ridibunda*-gebied. Dit is bovendien een jong exemplaar (KBIN. 3848 - Ploegsteert).

3. BESLUITEN

Het onderzoek van 124 gefixeerde zgn. *R. esculenta*-exemplaren, verspreid over gans België, leidt tot volgende vaststellingen :

1° zowel naar vorm van de metatarsale knobbel als naar de relatieve afmetingen van tibia en metatarsale knobbel kunnen 9 exemplaren met enige zekerheid als *lessonae* bestempeld worden;

2° één juveniel exemplaar uit Ploegsteert lijkt naar beide criteria *ridibunda* te zijn.

3° het overgrote deel (63 %) der exemplaren werd op zicht als *esculenta* gerangschikt. Slechts 39 % zijn zowel op zicht, als naar verhoudingen betrouwbaar gerangschikt

4° 29 % der specimens worden op zicht als intermediaire vormen gerangschikt.

5° voortgaande op deze resultaten, maar in acht nemend dat het aantal waarnemingen gering is, dat slechts 3 criteria werden gebruikt, en dat andere belangrijke aanduidingen zoals vorm van schedel, kleur en vlekkenpatroon niet werden beschouwd, is het voorkomen in België van *R. lessonae* zeer waarschijnlijk.

Verder onderzoek zal moeten uitwijzen of ook *R. ridibunda* inderdaad voorkomt zoals gesuggereerd door één exemplaar.

TABEL II

Materiaallijst

2.1. Specimens, naar vorm van metatarsale knobbel én naar verhoudingen : *Rana lessonae.*

Reg. nr.	Vindplaats en datum	RL	TIB	TC	Te 1	Type TC	Ratio Type	Sex
1322	Genk, Lim, VI.1943	55.3	23.4	4.0	6.9	L	L	F
1532	Hofstade, IV.1944	41.0	17.4	3.3	5.0	L		J
1674	Kalmthout, Ant., IX.1945	60.6	24.7	4.5	7.3	L	L	F
3844	Reningelst, WVl, VI.1956	67.7	28.7	4.6	7.8	L	L	F
3849	Wervik, WVl, 2.VIII.1956	54.1	24.3	4.4	6.5	L	L	M
B85	Muizen, Bra, 17.V.1971	54.2	24.7	4.0	7.3	L	L	M
B88	Muizen, Bra, 17.V.1971	47.4	22.1	3.9	6.4	L	L	M
B91	Arendonk, Ant, 9.VIII.1971	59.1	26.0	4.5	7.1	L	L	F
B108	Ruisbroek, 26.VII.1971	40.2	16.8	3.5	4.8	L	L	FJ

2.2. Specimen, naar vorm en naar verhoudingen : *Rana ridibunda.*

Reg. nr.	Vindplaats en datum	RL	TIB	TC	Te 1	Type TC	Ratio Type	Sex
3848	Ploegsteert, VIII.1956	38.5	18.0	1.8	5.2	R	R	J

2.3. Specimens, naar vorm en/of naar verhoudingen : « *esculenta* » en/of intermediair.

Reg. nr.	Vindplaats en datum	RL	TIB	TC	Te 1	Type TC	Ratio Type	Sex
616	Suzeril, VIII.1939	74.8	33.0	4.5	9.3	E	LE	—
618	Suzeril, IV.1940	57.7	27.0	4.1	6.8	E	LE	F
768	Oelegem, Ant, V.1942	47.8	23.6	3.3	6.7	E	LE	—
769	Oelegem, Ant, V.1942	58.8	27.9	3.6	8.2	E	E	—
769	Oelegem, Ant, V.1942	52.1	24.4	3.5	7.5	E	LE	—
769	Oelegem, Ant, V.1942	47.9	22.5	3.0	6.3	E	E	—
843	Carlsburg, Lux, VIII.1928	55.5	25.9	3.8	8.2	E	LE	F
843	Carlsburg, Lux, VIII.1928	43.3	19.8	3.1	5.9	E	LE	—
844	Graide, Nam, VIII.1928	52.8	24.1	4.4	7.3	LE	E	M
844	Graide, Nam, VIII.1928	44.1	19.9	2.9	6.5	LE	LE	M

Reg. nr.	Vindplaats en datum	RL	TIB	TC	Te 1	Type TC	Ratio Type	Sex
845	Carlsburg, Lux, VIII.1928	47.5	22.5	3.5	8.2	LE	LE	—
847	Wavreille, VII.1942	49.8	19.9	3.7	5.6	E	L	—
1203	Wavreille, VI.1943	46.5	19.2	3.5	5.9	LE	L	J
		42.7	18.0	3.2	5.2	LE	L	J
		48.3	22.2	3.8	6.1	LE	L	M
		39.5	16.9	2.6	5.0	LE	LE	J
1322	Genk, Lim, VI.1943	49.7	20.6	3.6	4.6	E	L	F
		46.1	18.3	3.2	5.3	LE	L	FJ
1530	Kortrijk, WVL, V.1944	72.0	34.5	5.6	10.9	E	LE	M
1531	Kortrijk, WVL, V.1944	74.0	34.0	4.7	10.6	ER	E	F
1532	Hofstade, IV.1944	50.7	23.0	3.8	7.6	LE	LE	M
1671	Mans, III.1945	58.5	25.6	4.6	7.8	LE	L	F
1992	Tervuren, Bra, IV.1946	53.0	24.5	3.6	7.8	E	LE	M
2087	Neerlinter, VII.1949	64.5	32.4	4.3	9.0	E	LE	F
2612	Oudergem, Bra, VI.1948	32.2	14.1	2.2	4.2	E	LE	—
3841	Beveren, WVL, 16.V.1956	56.4	25.1	3.9	8.0	E	LE	F
		60.4	27.3	4.3	9.5	LE	LE	F
		57.8	26.4	4.0	7.6	E	LE	M
		60.0	27.7	4.6	8.2	E	L	F
3842	Proven, WVL, V.1956	77.1	33.8	4.6	9.0	E	E	F
		46.4	20.6	2.6	6.6	E	E	J
3843	Westouter, WVL, VI.1956	55.0	23.9	3.8	7.0	E	L	M
		55.0	25.2	3.8	7.2	E	LE	M
		42.3	19.5	2.8	5.8	E	LE	J
3844	Reningelst, WVL, VI.1956	61.7	26.7	4.1	7.3	LE	LE	F
		58.0	25.9	4.0	7.6	LE	LE	F
3846	Leysele, VI.1956	59.8	26.8	4.1	8.5	E	LE	F
3847	St. Léger, Hen, VIII.1956	46.7	21.4	2.9	6.5	E	E	F
		37.5	18.6	2.2	5.2	ER	E	—
		37.7	17.8	2.3	5.1	ER	E	—
3849	Wervik, WVL, 2.VIII.1956	66.5	30.8	3.7	8.7	E	E	F
3849	Wervik, WVL, 2.VIII.1956	58.5	28.1	3.6	8.5	E	E	M
		63.5	28.9	3.7	7.8	E	E	F
		56.5	26.8	3.2	7.6	ER	E	F
		56.1	26.8	3.3	7.9	E	E	M
		54.3	25.0	3.3	7.9	E	E	M
		52.9	24.7	3.2	7.7	E	E	M
		54.0	26.2	3.0	8.5	ER	ER	M
		52.1	25.3	3.1	7.4	E	E	M
		56.5	24.4	3.6	7.7	E	LE	M
4792	Brasschaat, Ant, V.1961	49.9	21.2	4.0	5.7	E	L	M
		39.4	16.7	2.8	4.5	E	L	FJ
7059	Metzert, VI.1966	54.0	24.4	3.8	7.1	E	L	F
		65.1	28.4	4.4	8.5	LE	LE	M
7059	Dareheck, Metzert, VI.1966	57.0	25.6	4.2	7.6	E	L	M

Reg. nr.	Vindplaats en datum	RL	TIB	TC	Te 1	Type TC	Ratio Type	Sex
7367	Brecht, Ant, III.1968	65.2	29.9	4.5	8.8	LE	LE	M
		54.5	23.2	4.5	5.7	E	L	M
		56.3	24.8	4.4	7.8	E	L	F
		43.4	18.7	3.1	5.5	E	L	J
7572	Eigenbilzen, VII.1968	58.4	23.7	4.0	7.4	E	L	F
		40.3	19.0	2.9	5.6	E	LE	J
7572	Eigenbilzen, VII.1968	43.1	22.3	2.9	7.0	E	E	F
7573	Eigenbilzen, VII.1968	41.1	20.2	3.0	5.9	E	LE	J
7574	Scherpenberg-Berenbroek	58.8	28.6	4.2	8.4	E	LE	F
	VII.1968	46.3	22.2	3.1	6.6	E	E	—
7766	Rekkem, Lim, VII.1968	37.8	16.9	2.9	5.4	E	L	—
		34.1	15.0	2.5	5.0	E	LE	—
7767	Bolderberg, Zandhoven,	49.0	24.2	3.0	7.5	ER	E	—
	VIII.1968	42.1	20.1	2.7	6.3	E	E	—
		55.3	25.9	3.9	8.4	E	LE	M
		43.7	20.7	2.7	6.3	ER	E	—
		39.0	18.3	2.8	5.9	E	LE	—
		41.1	19.5	2.5	6.4	ER	E	—
		41.1	18.8	3.1	5.6	E	L	—
7774	Zutendael, VIII.1968	47.4	20.8	3.6	6.3	E	L	M
	id.	42.5	19.4	3.0	5.2	E	L	F
	id.	34.2	14.8	2.3	4.5	E	LE	J
7775	Gellik, Lim, VII.1968	39.8	19.0	2.8	5.8	E	LE	—
7776	Mechelen a. Maas, VII.1968	50.6	22.4	3.8	7.0	E	L	—
	id.	42.7	19.4	3.5	5.5	E	L	—
	id.	35.5	15.7	2.6	5.0	E	LE	J
7777	Zutendael, VII.1968	54.3	24.6	3.9	7.3	LE	L	F
7778	Zutendael, Lim, VII.1968	48.1	22.7	2.8	7.0	ER	E	—
	id.	49.2	23.3	2.9	7.4	ER	E	F
7779	Loutte St. Pierre, Nam.	52.0	22.5	3.5	6.4	E	L	F
B25	Niel, OV.IV.1971	59.6	28.1	3.7	8.2	E	E	F
B75	Muizen, Bra, 17.V.1971	57.2	28.6	3.7	7.8	E	E	M
B76	id.	59.5	29.8	4.0	8.7	E	E	M
B77	id.	54.0	26.1	4.2	7.2	LE	L	M
B78	id.	58.0	28.8	4.0	8.4	LE	E	M
B79	id.	58.0	29.2	3.7	8.5	E	E	M
B80	id.	59.1	29.3	4.0	8.2	E	LE	M
B81	id.	56.9	28.4	3.5	8.7	E	E	M
B82	id.	52.5	25.2	3.1	7.2	E	E	M
B86	id.	62.8	29.0	4.1	8.8	LE	E	M
B92	?	48.0	22.3	3.2	6.4	LE	LE	J
B93	Arendonk, Ant, 09.VIII.71	69.5	33.6	5.0	8.7	LE	LE	M
B94	Basel, OVL, 10.VIII.1971	62.8	31.2	3.7	9.9	E	E	M
B102	Genk, Lim, 22.VI.1971		23.3	3.6	6.8	LE	L	F
B103	Rekem, 23.VI.1971	47.1	21.3	3.3	6.5	LE	LE	J

Reg. nr.	Vindplaats en datum	RL	TIB	TC	Te 1	Type TC	Ratio Type	Sex
B106	Arendonk, Ant, 19.VIII.71	57.3	25.5	3.6	8.0	E	E	M
B107	Arendonk, Ant, 04.VIII.71	48.2	22.4	3.3	6.4	LE	LE	J
B109	Hombeek, 26.VII.1971	55.5	25.7	3.6	7.7	LE	E	F
B110	Hombeek, 26.VII.1971		19.8	3.0	6.0	LE	LE	J
B111	Kapellen-Bos, 26.VII.1971	53.8	24.7	3.2	7.6	E	E	M
B126	Turnhout, Ant, 11.XII.1971	60.2	30.6	4.5	8.8	LE	LE	M

Nota : de reg. nrs. voorafgegaan door letter B behoren tot de RUCA-kollektie, de andere tot de kollekties van het K.B.I.N.
RL = romplengte, TIB = tibialengte, TC = metatarsale knobbellengte, Tel = teen 1 lengte, type TC = metatarsaal knobbeltype, Ratio type = type volgens fig. 1.
M = mannetje, F = wijfje, J = juveniel.

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CONTRIBUTION À L'ÉTUDE ZOOGÉOGRAPHIQUE DE L'ENTRE-SAMBRE-ET-MEUSE ET ANALYSE PARTICULIÈRE D'UN RUISSEAU (*)

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RÉSUMÉ

Une recherche zoogéographique dans l'Entre-Sambre-et-Meuse basée sur l'utilisation du réseau U.T.M. 5 km, a permis de constater que *Dugesia gonocephala*, *Erpobdella octoculata*, *Lymnaea peregra* f. *ovata* et *Ancylus fluviatilis* étaient très répandus dans la région. L'utilisation du réseau U.T.M. 1 km dans l'étude du ruisseau de Fosses a mis en évidence, parmi les espèces étudiées, différents types de répartition. Après comparaison de ces données avec les analyses physico-chimiques effectuées sur ce même ruisseau, nous avons repéré une zone de pollution de type organique et chimique. Il semble y avoir une relation entre cette pollution et l'élimination de quelques espèces aquatiques telles que *D. gonocephala*. *E. octoculata* et *L. peregra* semblent plus tolérantes vis-à-vis de cette pollution.

SUMMARY

A zoogeographic investigation, using the U.T.M. 5 km squaring, establishes the wide distribution of *Dugesia gonocephala*, *Erpobdella octoculata*, *L. peregra* f. *ovata* and *A. fluviatilis* in the Entre-Sambre-et-Meuse district. Nowever a more refined examination of the « ruisseau de Fosses » by way of the U.T.M. 1 km squaring, makes obvious discontinuities in the distribution of some of these species. Comparing these data with the results of physico-chemical analysis of this streamlet, we were able to localize a zone of organic and chemical pollution. It seems to be a relation between these kinds of pollution and the disappearance of some aquatic species such as *D. gonocephala*, while *E. octoculata* and *L. peregra* show a higher degree of tolerance.

INTRODUCTION

Le souci d'une bonne représentation graphique de la distribution des organismes vivants a beaucoup préoccupé les biogéographes ces dernières décennies (Turrill et al. 1954 ; Gaspar 1971 ; Leclercq 1973). En 1965, le système « Universal Transverse Mercator » (U.T.M.) a été préconisé par les phytogéographes et zoogéographes européens. J. Heath et J. Leclercq ont établi un projet de « Cartographie des Invertébrés européens ». Ces auteurs ont adopté un modèle standardisé de cartes à

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réseau du type U.T.M. qui divise l'Europe en carrés de 100 - 50 - 10 km de côté (GASPAR, 1971). Ce système de quadrillage a l'avantage direct de permettre des découpages en carrés de plus en plus réduits, tous désignés selon un code standardisé (LECLERCQ, 1975).

Ces cartes constituent une base de travail pour poser des questions, formuler des hypothèses. Elles sont également un outil en vue d'une bonne gestion de l'environnement (LECLERCQ, 1975). Elles permettent de mettre en évidence les régressions ou les expansions de certaines espèces, souvent en relation avec une modification de l'environnement.

En ce qui concerne la qualité des eaux courantes, de nombreux modes de surveillance sont préconisés actuellement mais ils sont basés principalement sur les caractères physico-chimiques de l'eau. Si l'analyse physico-chimique est une approche indispensable, son interprétation reste souvent délicate car les résultats varient selon les rejets, les méthodes d'analyses et les laboratoires. De plus, on crée sans cesse de nombreuses nouvelles substances chimiques qui risquent d'altérer la qualité des eaux et pour lesquelles il n'existe pas encore de méthodes de dosages adéquates. Il est donc indéniable que les méthodes biologiques sont un complément utile aux méthodes chimiques par le simple fait que la présence ou l'absence des organismes résulte d'une véritable intégration continue de l'ensemble des paramètres physico-chimiques de l'eau dans laquelle ils vivent et cela sur la durée de leur cycle vital (VERNEAUX et LEYNAUD, 1974 ; MICHA, 1975).

Cette étude dans onze ruisseaux de l'Entre-Sambre-et-Meuse, tend à montrer l'intérêt de la démarche zoogéographique dans la connaissance de la qualité des eaux courantes ; elle a deux objectifs principaux :

— l'élaboration des cartes de distribution de quelques espèces aquatiques dans la région considérée ;

— la mise en évidence des principales zones polluées d'un cours d'eau à partir de la répartition des organismes recherchés et d'analyses physico-chimiques.

1. RÉGION ÉTUDIÉE

L'étude zoogéographique concerne la région de l'Entre-Sambre-et-Meuse qui s'étend de 4°37′ à 4°53′ longitude Est et de 50°14′ à 50°28′ latitude Nord. La région prospectée couvre approximativement 600 km².

Du point de vue géologique, cette région est constituée d'une alternance de couches calcaires, grès et schistes. L'altitude varie de 300 m à 90 m. Le couvert végétal présente quelques zones de forêts caducifoliées et de conifères. Mais cette région est essentiellement agricole. D'autre part, quelques carrières se sont implantées le long de certains ruisseaux.

Dans le réseau hydrographique de l'Entre-Sambre-et-Meuse, nous étudions, principalement, parmi les affluents de la Meuse : la Marlagne (H), le Burnot (L), le ruisseau d'Annevoie (M) et la Molignée (N) (fig. 1) ; parmi les affluents de la Sambre : le Landoir (C), le ruisseau de Floreffe (D), le ruisseau de Godronval (F) et le ruisseau de Fossés (G). Ces ruisseaux appartiennent au rhithron. Leur pente moyenne est de 1 à 3 % et la plupart d'entre eux ne présentent pas de rupture de pente très marquée.

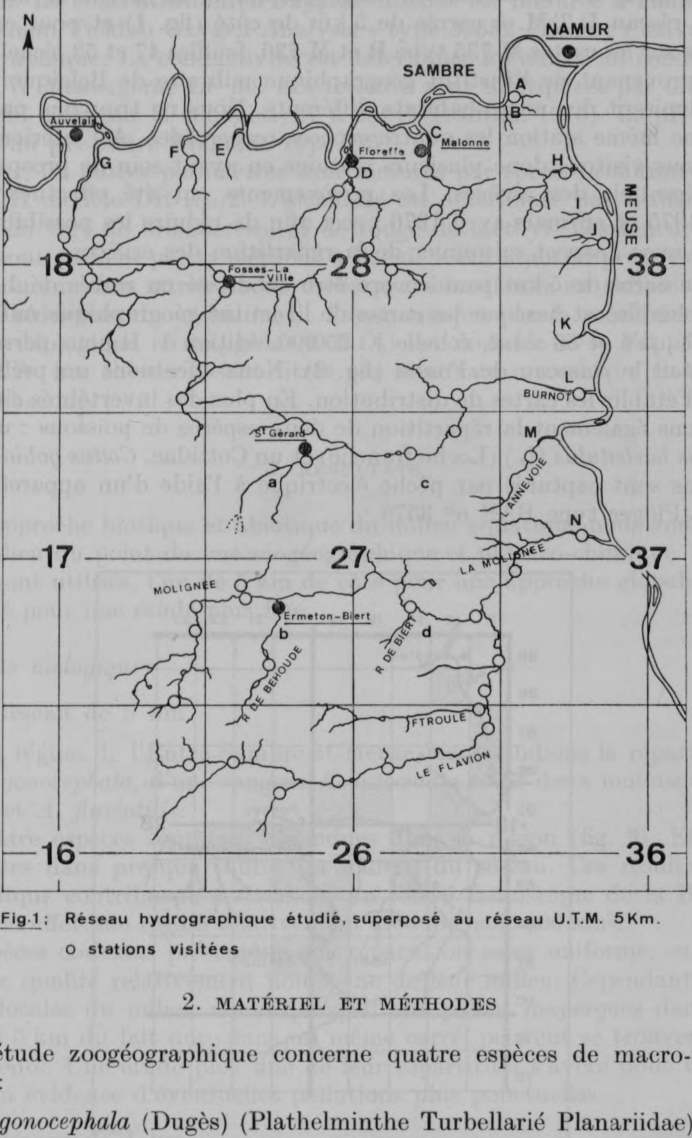

Fig.1 : Réseau hydrographique étudié, superposé au réseau U.T.M. 5 Km.

○ stations visitées

2. MATÉRIEL ET MÉTHODES

Notre étude zoogéographique concerne quatre espèces de macro-invertébrés aquatiques :

— *Dugesia gonocephala* (Dugès) (Plathelminthe Turbellarié Planariidae)

— *Erpobdella octoculata* (L.) (Annélide Hirudinée Erpobdellidae)

— *Lymnaea peregra* (Müll.) forma *ovata* (Drap.) (Mollusque gastéropode basommatophore Lymnaeidae)

— *Ancylus fluviatilis* (Müll.) (Mollusque gastéropode basommatophore Ancylidae).

Ces quatre espèces sont facilement identifiables sur le terrain. Le matériel utilisé pour leur récolte est simple : un filet troubleau métallique d'un diamètre de mailles de 1 cm, entouré d'un filet tissé à mailles de 1 mm. La faune pétricole est prélevée manuellement. Le prélèvement est effectué durant 30 minutes sur un secteur de 50 m. Le tri s'effectue le plus souvent sur le terrain.

Comme mode de représentation zoogéographique au niveau de la région, nous utilisons le réseau U.T.M. à carrés de 5 km de côté (fig. 1) et pour ce faire, nous nous basons sur les cartes M-735 type R et M-736, feuilles 47 et 53, échelle 1 : 50.000, édition 1, provenant de l'Institut géographique militaire de Belgique. Les espèces choisies colonisent des micro-habitats différents. Nous ne trouvons pas nécessairement en une même station les quatre espèces recherchées. A l'intérieur d'un carré de 5 km, nous visitons donc plusieurs stations en ayant soin de prospecter les biotopes préférentiels des espèces. Les prélèvements ont été effectués en octobre-décembre 1975 et en mars-avril 1976 ; ceci afin de réduire les possibilités d'erreurs en relation avec l'aspect saisonnier de la répartition des espèces.

Chaque carré de 5 km peut encore être subdivisé en carrés de 1 km de côté. Ce réseau plus fin est basé sur les cartes de l'Institut géographique militaire M 834, planches 47 : 5-6 et 53 : 1-2, échelle 1 : 25.000, édition 1. Il nous permet d'étudier plus en détail le ruisseau de Fosses (fig. 2). Nous effectuons un prélèvement par carré afin d'établir les cartes de distribution. En plus des invertébrés cités ci-dessus, nous étudions également la répartition de deux espèces de poissons : un Cobitidae, *Nemacheilus barbatulus* (L.) (Loche franche) et un Cottidae, *Cottus gobio* L. (Chabot). Les poissons sont capturés par pêche électrique à l'aide d'un appareil portatif de marque F. Plöger type BAF n° 3575.

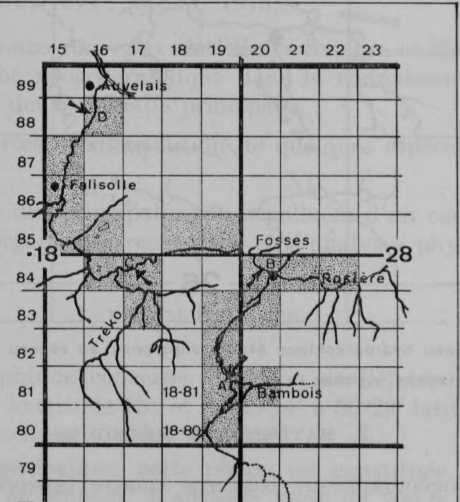

Fig. 2. — Tracé du ruisseau de Fosses dans le réseau U.T.M. 1 km
▨ : carrés visités pour analyses biologiques
A. B. C. D : stations pour analyses physico-chimiques.

Les mesures physico-chimiques de l'eau sont effectuées, les unes sur le terrain, les autres au laboratoire du Cebedeau à Liège et au laboratoire d'Ecologie Dulcicole à Namur. Les prélèvements ont été effectués le 14 avril 1976 en quatre points représentatifs du ruisseau de Fosses (fig. 2).

La température, la teneur en oxygène dissous et la conductivité sont mesurées sur le terrain. La concentration en oxygène dissous est mesurée à l'aide d'un oxymètre « Beckman Fieldab Oxygen Analyser » type 39552 « Sensor » suivant le principe polarographique. La conductivité est déterminée à l'aide d'un conductivimètre du type WTW Messergerät LF 56. Les mesures sont multipliées par un facteur de correction afin d'obtenir la conductivité à 20° C (RODIER, 1975). Le pH est mesuré au moyen d'un pH-mètre Beckman type H5.

A Namur, les autres paramètres sont mesurés par spectro-colorimétrie avec la trousse HACH modèle DR-EL/2. L'alcalinité est déterminée par titrage au H_2SO_4 en présence de vert de bromocrésol et de rouge de méthyl. Les teneurs en orthophosphates sont établies par la méthode à l'acide ascorbique en présence de molybdate d'ammonium. Les nitrites sont dosés par diazotation au sulfate ferreux, les nitrates par réduction du cadmium et l'ammoniaque par la méthode de Nessler. La demande biologique en oxygène ($D.B.O_5$) est mesurée avec l'appareil HACH modèle 2173 A. Les chlorures sont titrés par le nitrate mercurique en présence de diphényl carbazone.

3. RÉSULTATS

Notre approche biotique et abiotique du milieu aquatique nous amène à caractériser le milieu du point de vue zoogéographique et physico-chimique. Deux types de réseaux sont utilisés, l'un de 5 km de côté pour une approche globale, l'autre de 1 km de côté pour une étude plus fine.

3.1. *Résultats biologiques*

3.1.1. Réseau de 5 km

Dans la région de l'Entre-Sambre-et-Meuse, nous étudions la répartition d'une planaire *D. gonocephala,* d'une sangsue *E. octoculata* et de deux mollusques *L. peregra* f. *ovata* et *A. fluviatilis.*

Ces quatre espèces sont très répandues dans la région (fig. 3). Elles sont en effet présentes dans presque toutes les mailles du réseau. Ces résultats de type zoogéographique contribuent activement au relevé faunistique de la Belgique. Ils concernent en effet une région relativement étendue, soit 600 km^2.

Les espèces ci-dessus présentent une répartition assez uniforme, ce qui semble indiquer une qualité relativement homogène de leur milieu. Cependant, de petites altérations locales du milieu aquatique peuvent passer inaperçues dans le réseau à mailles de 5 km du fait que, dans un même carré, peuvent se trouver deux ruisseaux différents. Une étude plus fine de leur répartition s'avère donc utile en vue de mettre en évidence d'éventuelles pollutions plus ponctuelles.

3.1.2. Réseau de 1 km

Dans une partie du large réseau de l'Entre-Sambre-et-Meuse, en l'occurrence le ruisseau de Fosses, nous étudions plus en détail la répartition des quatre espèces de macro-invertébrés mentionnées ci-dessus et de deux espèces de poissons : *N. barbatulus* et *C. gobio.*

D. gonocephala est beaucoup moins bien représentée le long du ruisseau de Fosses (fig. 4) que ne pouvait le laisser prévoir la carte de répartition à mailles plus larges. Elle n'est signalée qu'en deux stations : en amont de Fosses-la-Ville (carré 19-83) et dans l'affluent « Le Tréko » (carré 17-83). Nous ne rencontrons plus cette espèce en aval de Fosses-la-Ville.

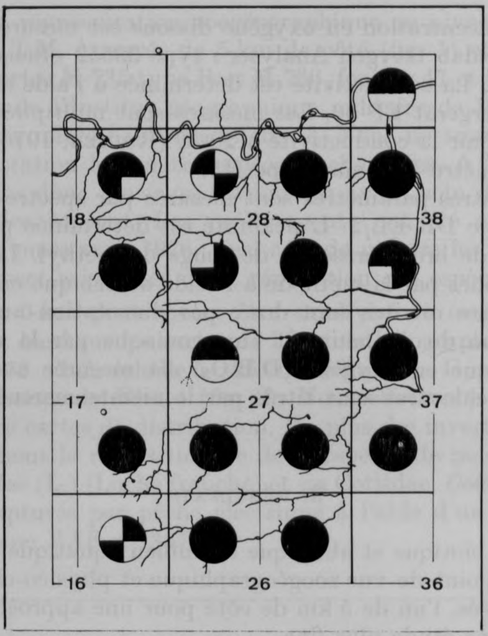

Fig. 3. Carte de répartition de Dugesia gonocephala ◴ , Erpobdella octoculata ◷ , Lymnaea peregra f. ovata ◵ , Ancylus fluviatilis ◶ dans la région (mailles de 5 km.)

E. octoculata est très largement répandue dans le ruisseau de Fosses (fig. 5). Nous la trouvons dans toutes les stations visitées excepté dans le carré 17-83.

L. peregra f. *ovata* a une répartition analogue à celle d'*E. octoculata* (fig. 6). Ce mollusque est présent dans presque toutes les stations y compris à Fosses (carré 20-84).

A. fluviatilis a une répartition moins large que *L. peregra* (fig. 7). Comme cette dernière, il est présent dans la moitié amont du ruisseau mais il est moins bien représenté dans le cours inférieur.

N. barbatulus (Loche franche) est présent dans la moitié amont du ruisseau à l'exception de trois stations en aval du lac de Bambois (carrés 19-81 et suivants) (fig. 8). Nous le trouvons à Fosses-la-Ville (carré 20-84) et en aval de cette ville (carrés 19-85 et suivants). Il n'est cependant plus signalé à partir du carré 15-85.

C. gobio (Chabot) semble moins répandu que *N. barbatulus* (fig. 9). Nous l'observons dans les deux principaux affluents du ruisseau : le ruisseau de la Rosière et le Tréko et en amont de Fosses (carré 19-83). Par contre, en aval de cette ville, nous ne le rencontrons plus qu'en une seule station distante d'environ 4 km (carré 16-84).

L'utilisation du réseau à mailles de 1 km met donc en évidence différents types de répartition longitudinale parmi les six espèces étudiées dans le ruisseau de Fosses. En effet, en amont de Fosses-la-Ville, les six espèces sont présentes. Dans la zone inférieure du ruisseau, deux seulement semblent subsister : *E. octoculata* et *L. peregra*. Cette modification dans la faune du ruisseau de l'amont vers l'aval pourrait résulter d'une altération réelle du milieu aquatique à partir de Fosses.

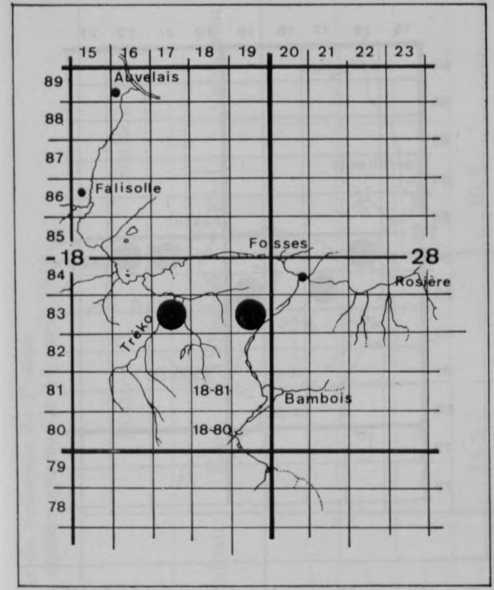

Fig. 4. — Carte de répartition de *Dugesia gonocephala* le long du ruisseau de Fosses (mailles de 1 km).

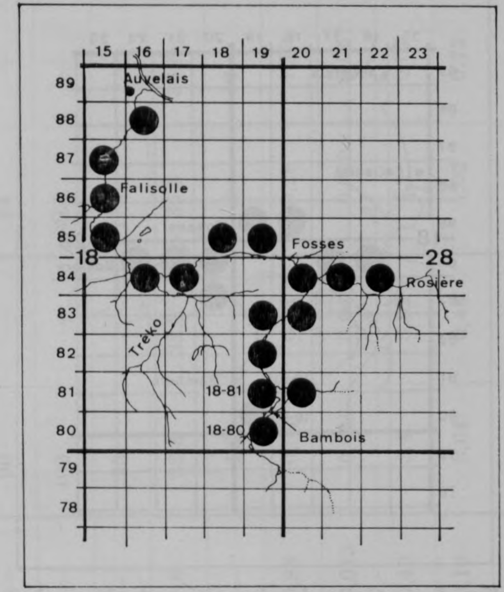

Fig. 5. — Carte de répartition d'*Erpobdella octoculata* le long du ruisseau de Fosses (mailles de 1 km).

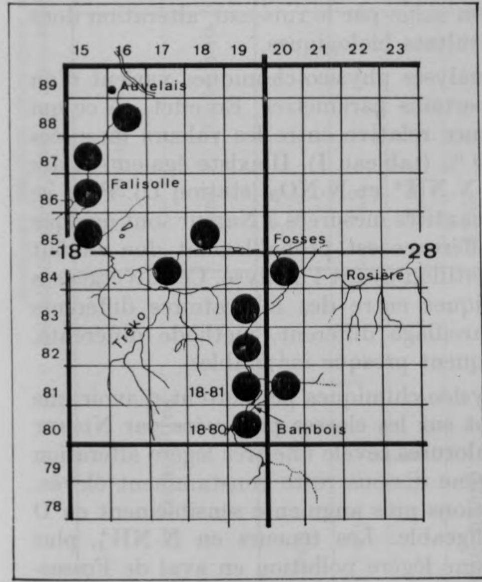

Fig. 6. — Carte de répartition de *Lymnaea peregra* f. *ovata* le long du ruisseau de Fosses (mailles de 1 km).

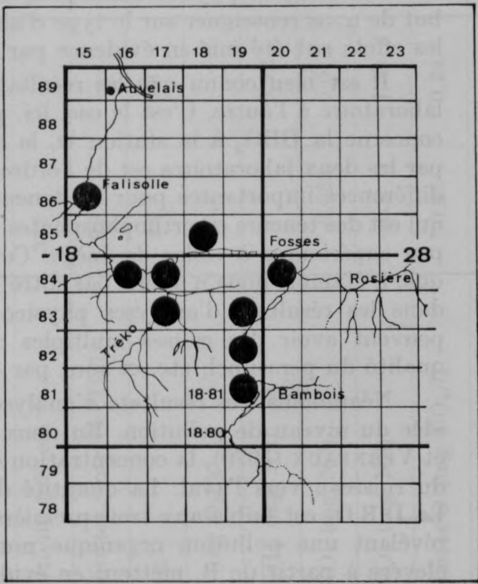

Fig. 7. — Carte de répartition d'*Ancylus fluviatilis* le long du ruisseau de Fosses (mailles de 1 km).

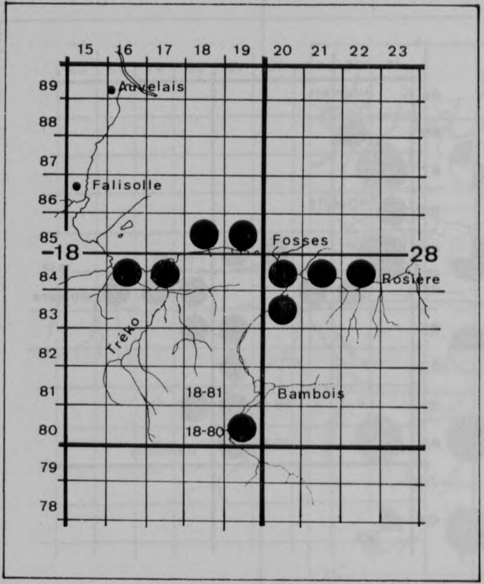

Fig. 8. — Carte de répartition de *Nemacheilus barbatulus* le long du ruisseau de Fosses (mailles de 1 km).

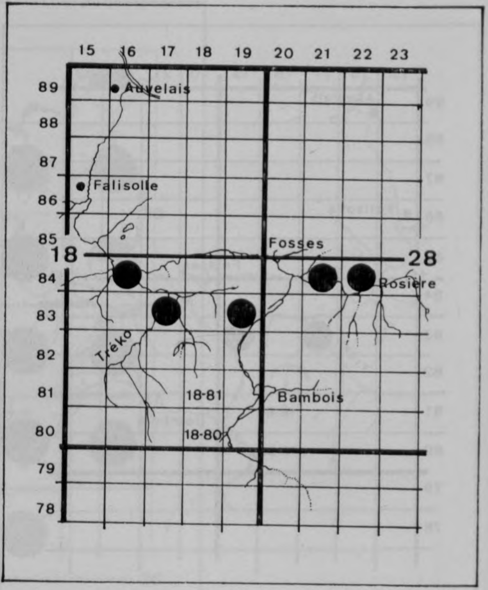

Fig. 9. — Carte de répartition de *Cottus gobio* le long du ruisseau de Fosses (mailles de 1 km).

3.2. *Résultats physico-chimiques*

Les analyses physico-chimiques, effectuées dans le ruisseau de Fosses, ont pour but de nous renseigner sur le type d'altération subie par le ruisseau, altération dont les effets ont été mis en évidence par les résultats biologiques.

Il est bien connu que les résultats d'analyses physico-chimiques varient d'un laboratoire à l'autre. C'est le cas, ici, pour certains paramètres. En effet, en ce qui concerne la DBO_5 à la station D, la différence relative entre les valeurs mesurées par les deux laboratoires est de l'ordre de 50 % (tableau I). Il existe également des différences importantes pour les teneurs en $N\text{-}NH^+$ et $N\text{-}NO_3$ (station D). Pour ce qui est des teneurs en orthophosphates, les quantités mesurées à Namur sont quelque peu supérieures à celles de Liège. Cette différence est probablement due au fait que, à Namur, nous n'avons pas filtré l'échantillon avant l'analyse. Ces divergences dans les résultats d'analyses physico-chimiques entre des laboratoires différents peuvent avoir des causes multiples : appareillage différent, méthode différente, qualité du personnel, etc. et sont par conséquent presque inévitables.

Néanmoins, ces résultats d'analyses physico-chimiques permettent d'avoir une idée du niveau de pollution. En nous basant sur les classes proposées par NISBET et VERNEAUX (1970), la concentration des chlorures révèle une très légère altération du ruisseau vers l'aval. La quantité d'oxygène dissous reste constamment élevée. La $D.B.O_5$ est faible aux trois premières stations puis augmente sensiblement en D révélant une pollution organique non négligeable. Les teneurs en $N\text{-}NH_4^+$, plus élevées à partir de B, mettent en évidence une légère pollution en aval de Fosses-la-Ville. Les nitrites augmentent sensiblement à la station D révélant une certaine altération de la qualité de l'eau. Les nitrates augmentent d'amont en aval surtout en B et en C et traduisent une certaine eutrophisation. La concentration en phosphates totaux est également élevée, signe d'une eutrophisation du milieu.

TABLEAU I

Analyses physico-chimiques aux quatre stations du ruisseau de Fosses
(résultats correspondant à un seul prélèvement par station effectué le 14 *avril* 1976*)*

Paramètres	Station A		Station B		Station C		Station D	
	Ecol.	Cebedeau	Ecol.	Cebedeau	Ecol.	Cebedeau	Ecol.	Cebedeau
t° air (°C)	8	—	7	—	6	—	7	—
t° eau (°C)	6,3	—	6,0	—	6,2	—	6,4	—
pH	8,48	—	8,40	—	8,30	—	8,21	—
Oxygène (ppm)	12,6	—	10,1	—	11,3	—	10,3	—
% sat. oxygène	106	—	83	—	90	—	84	—
Conductivité ($\mu S.cm^{-1}$)	365	—	397	—	409	—	445	—
Alcalinité tot. (mg.$CaCO_3$/l)	98	—	94	—	95	—	110	—
Cl^- (mg/l)	25	25,3	32,5	31,8	32,5	32,3	35,5	36,5
DBO_5 (mg O_2/l)	1,9	—	2	—	1,2	—	5	10
$N — NH_4^+$ (mg N/l)	0	0,12	0,32	0,88	0,06	0,74	0,28	1,10
$N — NO_2$ (mg N/l)	0,025	0,013	0,028	0,013	0,035	0,045	0,069	0,057
$N — NO_3$ (mg N/l)	1,8	1,44	4,9	5,49	5,4	5,82	4,1	0,07
Phosphates-O (mg PO_4/l)	0,27	0,24	0,66	0,10	0,64	0,48	1,02	0,72
Phosphates-O + Poly (mg PO_4/l)	—	1,28	—	0,68	—	1,08	—	1,80

En résumé, les analyses physico-chimiques effectuées sur le ruisseau montrent qu'une pollution organique et chimique altère le milieu à partir de Fosses. Les altérations sont dans l'ensemble de faible importance et la station D paraît la plus touchée.

4. DISCUSSION ET CONCLUSION

L'utilisation du réseau U.T.M.-5 km a fourni des résultats de type zoogéographique. Les cartes de répartition des quatre espèces de macro-invertébrés étudiées ont montré qu'elles étaient très répandues dans la région. La technique utilisée ici n'a mis en évidence que le facteur présence-absence des espèces dans chaque carré et ceci, compte tenu de l'effort de capture réalisé. Cependant, ces données zoogéographiques ont un intérêt certain dans l'inventaire faunistique de la Belgique. En effet, il semble y avoir très peu de renseignements dans la littérature concernant la répartition en Belgique de *Dugesia gonocephala* et de *Erpobdella octoculata*. En ce qui concerne *Ancylus fluviatilis*, ADAM (1947-1960) le mentionne dans presque tout le pays à l'exception de la Flandre occidentale. D'après la carte de répartition que cet auteur donne, cette espèce serait peu répandue dans la partie de l'Entre-Sambre-et-Meuse que nous avons étudiée. Notre recherche zoogéographique a donc fourni des renseignements complémentaires utiles puisque, à la suite de notre étude, nous pouvons dire que *A. fluviatilis* est largement répandu dans la région. *Lymnaea peregra* est renseignée par ce même auteur presque exclusivement en Ardennes. La forme *ovata*, actuellement associée à l'espèce *peregra*, semble très largement répandue en Belgique (ADAM, 1947) mais l'étude que nous avons menée a fourni quelques renseignements supplémentaires sur la répartition de ce Lymnaeidae dans l'Entre-Sambre-et-Meuse.

D'un point de vue écologique, les résultats obtenus à partir du réseau U.T.M.-5 km nous suggèrent qu'aucune pollution importante n'altère le milieu aquatique dans la région considérée. L'utilisation d'un réseau à larges mailles présente donc un intérêt à deux points de vue : d'abord sur le plan purement zoogéographique à l'échelle de la Belgique, ensuite dans un relevé des zones de pollution grave dans une région.

Des pollutions mineures étant difficilement détectées par un réseau à larges mailles, il nous faut aller plus loin dans notre étude de répartition pour les mettre en évidence. L'étude du ruisseau de Fosses, basée sur le quadrillage U.T.M.-1 km a ainsi permis de mettre en évidence des pollutions légères relativement localisées. Parmi les quatre macro-invertébrés étudiés, deux espèces se maintiennent tout le long du ruisseau, ce sont *E. octaculata* et *L. peregra*. *A. fluviatilis* est absent sur une courte distance en aval de Fosses-la-Ville et à hauteur de Falisolle et d'Auvelais. *D. gonocephala* est totalement absente en aval de Fosses. Les deux poissons étudiés ont une répartition quelque peu différente également : *N. barbatulus* est largement répandu dans le cours moyen du ruisseau. *C. gobio*, par contre, est présent en amont de Fosses puis disparaît en aval sur une longue distance. Il est à noter qu'aucun poisson ne subsiste dans la portion avale du ruisseau à hauteur de Falisolle et d'Auvelais. Il semble donc y avoir un appauvrissement de la faune vers l'aval.

D'après les mesures physico-chimiques effectuées sur le ruisseau de Fosses, il est apparu que les stations B, C et surtout D sont affectées. La station B se situe à la sortie de Fosses-la-Ville. Le ruisseau est déjà, à cet endroit, chargé en matières organiques. La station D se situe entre Falisolle et Auvelais ; le ruisseau subit l'effet de décharges chimiques et ménagères de la population riveraine. Cependant, l'approche physico-chimique présente certaines limites. Outre les différences observées entre les résultats fournis par deux laboratoires différents pour un même prélèvement, il est évident que les paramètres physico-chimiques connaissent de fortes variations quotidiennes, saisonnières et même annuelles. Par conséquent, les résultats d'analyses physico-chimiques ne donnent que des indications ponctuelles dans le temps. Un troisième inconvénient des analyses physico-chimiques concerne le manque de référence pour l'interprétation des niveaux de pollution. Nous avons choisi, pour cette étude, les références de base établies par NISBET et VERNEAUX. Mais ce sont des critères qui concernent une région de France et qui ne sont pas nécessairement applicables dans nos régions.

Néanmoins, si nous mettons en parallèle les résultats physico-chimiques et biologiques obtenus sur le ruisseau de Fosses, nous pouvons faire quelques observations. A la station B, relativement suspectée par les analyses physico-chimiques, *D. gonocephala* et *C. gobio* semblent disparaître. Ce dernier réapparaît à quelques kilomètres en aval de B. A la station D, considérée comme polluée à la suite des résultats physico-chimiques, deux seulement des six espèces étudiées semblent se maintenir : *E. octoculata* et *L. peregra.*

Nous voyons donc qu'il y a relation entre les résultats physico-chimiques et les résultats biologiques. Des renseignements plus précis seraient obtenus si nous tenions compte de l'abondance relative des espèces et si nous utilisions un système U.T.M. encore plus fin. Mais nous pouvons déjà affirmer qu'à partir de Fosses-la-Ville (station B), la pollution est de type organique et chimique et qu'elle est suffisante pour éliminer certaines espèces animales aquatiques, ce qui constitue un signal d'alarme pour l'observateur.

Dans le réseau étudié, *D. gonocephala*, classée par SLADECEK (1973) dans les zones xéno- et oligosaprobes, paraît effectivement peu résistance à la pollution ; cette espèce pourrait constituer un bon bioindicateur de pollution. *E. octoculata*, classée dans la zone α-mésosaprobe et *L. peregra* paraissent résistantes. *A. fluviatilis*, généralement signalé dans les eaux propres (GRASSE, 1968) ou peu polluées (SLADECEK, 1973), semble dans notre région relativement tolérant à une charge organique.

La méthode zoogéographique a donc un intérêt certain dans la surveillance de l'environnement. Par la présence ou l'absence d'espèces indicatrices, elle permet de mettre en évidence les zones les plus polluées et donc de diriger les efforts d'assainissement vers ces zones. Une étude zoogéographique continue permettrait également de vérifier l'amélioration de la qualité des eaux épurées en fonction de la réapparition d'espèces indicatrices dans les cours d'eau.

La méthode zoogéographique n'est cependant pas suffisante par elle-même dans une étude approfondie du degré d'altération d'un milieu. Non seulement, elle ne révèle pas l'élément polluant mais la répartition des animaux peut varier selon les saisons et l'absence d'une espèce en un point n'a pas nécessairement, comme cause unique, la pollution. Elle constitue cependant une approche utile dans la connaissance d'un milieu. La confrontation des renseignements d'ordre zoogéographique avec les données physico-chimiques permet d'avoir une bonne idée de l'état du milieu étudié.

REMERCIEMENTS

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Juillet 1979 (*Communication reçue le 20 mai 1978*)

APPORT DE L'INFORMATIQUE A L'ÉVALUATION BIOLOGIQUE DES SITES

par

R. R. TERCAFS (*)

RÉSUMÉ

Présentation des méthodes utilisées pour la gestion par l'informatique des données écologiques d'un territoire subnaturel de 2.000 hectares à Liège (Belgique).

Utilisation de coefficients synthétiques pour l'évaluation biologique des différents sites.

Simulation des altérations humaines.

Cartographie automatique.

Contribution of computer language to biological evaluation of territories

SUMMARY

Presentation of methods used for the management by computer of ecological data from a subnatural territory (2.000 hectares) in Liège (Belgium).

Use of synthetic coefficients for biological evaluation of different territories.

Simulation of human alterations.

Automatic mapping.

INTRODUCTION

Depuis quelques années, on assiste à un développement des études sur la gestion des territoires naturels et subnaturels par des méthodes chiffrées et objectives. Elles concernent de très vastes territoires (Tunisie : CHABERT, 1971 ; Argentine : MARLANGE, 1971), des sites très localisés (Limbourg belge : FROMENT et al., 1976 ; Sologne (France : GODRON et al., 1964) ou des applications spécialisées (exploitation forestière : RONDEUX, 1974). Ces recherches ont pour but de mettre à la disposition des aménageurs des éléments concrets leur permettant de mettre en place une politique de gestion la plus efficace possible compte tenu des objectifs désignés au préalable. Très rapidement, on s'est rendu compte que l'énorme masse des données à traiter nécessitait presqu'obligatoirement le recours à l'informatique, seule technique capable de maîtriser l'ensemble des problèmes posés. Ces nouvelles techniques spécialisées ont fait l'objet de plusieurs travaux (SMEDES, 1971 ; RONDEUX, 1974). Des synthèses générales ont également été publiées (USHER, 1973 ; LONG, 1974). Schématiquement, les caractères principaux de ces méthodes sont les suivants :

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— collecte systématique, ordonnée et objective des données sur le terrain,
— codification hiérarchisée des paramètres,
— conservation sur un support approprié (cartes, bandes magnétiques, etc.),
— traitement des données par un logiciel,
— mise au point de programmes d'interrogation,
— analyse des résultats,
— applications concrètes.

Ce schéma général se modifie évidemment suivant la nature des paramètres à récolter et des problèmes à résoudre.

C'est en suivant cette méthodologie générale que nous avons étudié le territoire dit des « 2.000 hectares », au Sart Tilman, qui constitue la pointe nord-est de l'Ardenne condrusienne. Ce territoire occupe donc une surface de 2.000 hectares dont environ le tiers (720 ha) a progressivement été acquis de 1960 à 1974 par l'Université de Liège afin d'y implanter un nouveau campus. Au niveau des problèmes posés par la gestion de ce territoire, on peut distinguer, par exemple :

— en urbanisme : choix de l'emplacement des bâtiments,
— en écologie : mise en réserve naturelle de certains sites,
— en information générale : mise à la disposition des utilisateurs des résultats des enquêtes détaillées.

L'ensemble de ces conditions, études sur le terrain largement entamées et forte demande d'informations, constitue un cas favorable pour une tentative de gestion des données par l'informatique. C'est pourquoi un plan de travail concerté a été mis en place en vue de constituer une *écothèque régionale*.

Suivant la définition proposée par Long (1974), une écothèque est constituée par un système de traitement par l'informatique des données écologiques, phytosociologiques, zoologiques, pédologiques, etc., récoltées dans un territoire donné. Elle implique aussi bien la saisie des données (perforation, etc.), que leur enregistrement (sous des formes compatibles et d'accès facile) et leur exploitation (recherches de renseignements, calculs, édition). Cette « banque de données » spécialisée est mise à la disposition des utilisateurs (aménageurs, écologistes, forestiers, etc.) et doit fournir des réponses rapides, précises et chiffrées.

C'est un aperçu des techniques de constitution et des systèmes d'interrogation utilisés pour constituer l'écothèque régionale du Sart Tilman qui est présenté ici. Le schéma général de l'organisation de l'écothèque est repris dans la figure 1. Bien entendu, la méthodologie expérimentée peut être largement reprise pour d'autres applications et dans d'autres sites.

MÉTHODOLOGIE

1. Le territoire à étudier est divisé en carrés numérotés (cases) ; la numérotation est associée à un système de coordonnées : les trois premiers chiffres désignent la ligne, les trois suivants désignent la colonne. Dans le cas du Sart Tilman, le nombre de cases est d'environ 32.000.

2. La surface d'une case unitaire est choisie en fonction de la surface occupée par le plus petit paramètre essentiel. Dans le cas présent, la case unitaire mesure 25 m de côté.

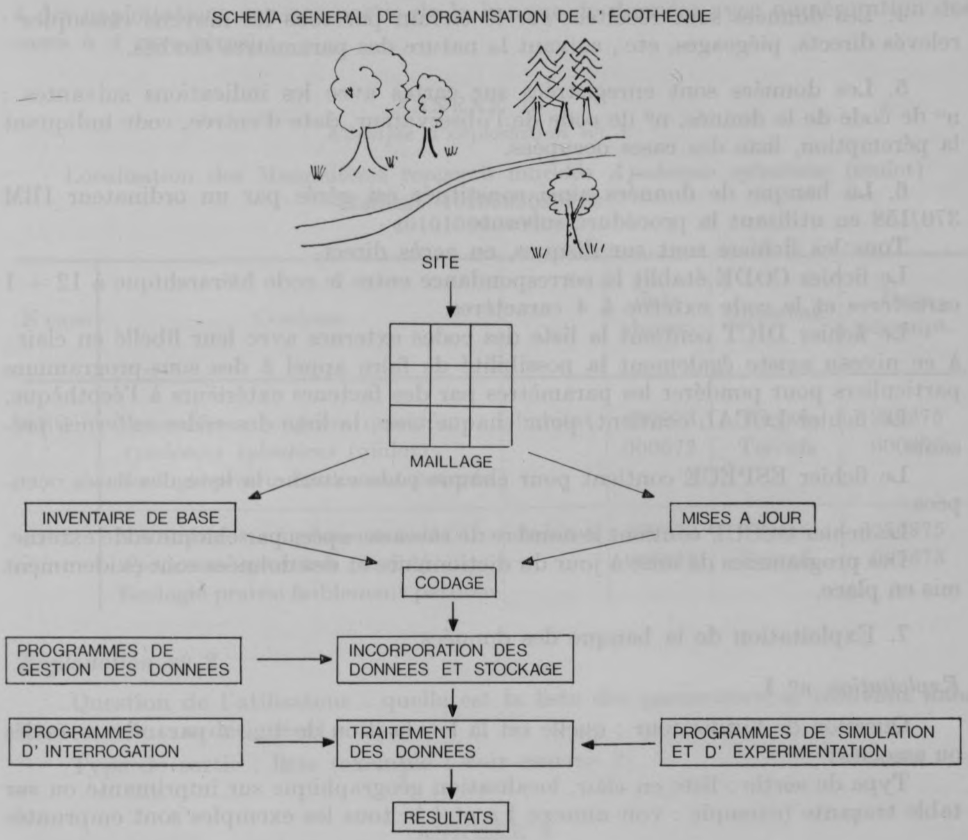

Fig. 1.

3. La forme des données est codifiées de la façon suivante afin de constituer un dictionnaire de paramètres à étudier :

- subdivision en catégories pouvant être traitées séparément : 1 = faunistique, 2 = floristique, 3 = phytosociologie, etc.
- dans chaque catégorie, un code hiérarchique à 12 caractères est établi.

Exemple : 01 = Mammifère, 0102 = Carnivore, 010201 = Canidé, 01020101 = *Vulpes*, 0102010101 = *Vulpes vulpes*, 01020101010110 = *Vulpes vulpes* habitat.

Ce système a pour buts :

- d'organiser les données de façon cohérente,
- de permettre l'utilisation d'un système d'interrogation hiérarchique.

Exemple : on pourra demander la localisation de toutes les données « Mammifères » ou d'une seule espèce « *Vulpes vulpes* habitat ».

Pour la facilité de la transcription et de l'entrée des données, chaque code à 12 + 1 caractères est transformé en code à 4 caractères dit « code externe ».

4. Les données sont récoltées sur le terrain par tous les moyens classiques : relevés directs, piégeages, etc., suivant la nature des paramètres étudiés.

5. Les données sont enregistrées sur cartes avec les indications suivantes : n° de code de la donnée, n° de code de l'observateur, date d'entrée, code indiquant la péremption, liste des cases occupées.

6. La banque de données ainsi constituée est gérée par un ordinateur IBM 370/158 en utilisant la procédure suivante :

Tous les fichiers sont sur disques, en accès direct.

Le fichier CODE établit la correspondance entre le code hiérarchique à 12 + 1 caractères et le code externe à 4 caractères.

Le fichier DICT contient la liste des codes externes avec leur libellé en clair ; à ce niveau existe également la possibilité de faire appel à des sous-programmes particuliers pour pondérer les paramètres par des facteurs extérieurs à l'écothèque.

Le fichier LOCAL contient, pour chaque case, la liste des codes externes présents.

Le fichier ESPÈCE contient pour chaque code externe la liste des cases occupées.

Le fichier OCCUP contient le nombre de cases occupées par chaque code externe.

Des programmes de mise à jour du dictionnaire et des données sont évidemment mis en place.

7. Exploitation de la banque des données.

Exploitation n° 1.

Question de l'utilisateur : quelle est la localisation de 1 ... *n* paramètres, isolés ou associés?

Type de sortie : liste en clair, localisation géographique sur imprimante ou sur table traçante (exemple : voir annexe 1 a et 1 b; tous les exemples sont empruntés

ANNEXE 1a
Exemple d'exploitation n° 1
Localisation des Mammifères rongeurs léporidés *Lepus europaeus* (Lièvre)
Habitat 1010501010110

N case	Contenu		date observ.	Observat.	Date prérempt.
0107	Mammifères rongeurs léporidés *Lepus europaeus* (lièvre)	habitat	060674	Tercafs	060675
0108	Mammifères rongeurs léporidés *Lepus europaeus* (lièvre)	habitat	060674	Tercafs	060675
0109	Mammifères rongeurs léporidés *Lepus europaeus* (lièvre)	habitat	060674	Tercafs	060675
0110	Mammifères rongeurs léporidés *Lepus europaeus* (lièvre)	habitat	060674	Tercafs	060675

à des exploitations sur une partie de la banque de données avec numérotation des cases à 4 caractères).

ANNEXE 1b

Exemple d'exploitation n° 1

Localisation des Mammifères rongeurs muridés *Apodemus sylvaticus* (mulot)
Habitat 1010503020110
4010100000000

N case	Contenu		date observ.	Observat.	Date pérempt.
0101	Mammifères rongeurs muridés *Apodemus sylvaticus* (mulot) Ecologie prairie faiblement paturée	habitat	230873 000673	Tercafs Tercafs	230875 000675
0102	Mammifères rongeurs muridés *Apodemus sylvaticus* (mulot) Ecologie prairie faiblement paturée	habitat	230873 000673	Tercafs Tercafs	230875 000675

Exploitation n° 2.

Question de l'utilisateur : quelle est la liste des paramètres se trouvant dans les cases 1 ... *n* désignées?

Type de sortie : liste (exemple : voir annexe 2).

ANNEXE 2

Exemple d'exploitation n° 2

0404	Mammifères rongeurs muridés *Apodemus sylvaticus* (mulot)	habitat	230873	Tercafs	230875
	Mammifères rongeurs muridés *Clethrionomys glareolus* (campagnol roux)	habitat	160873	Tercas	160875
	Oiseaux falconidés *Buteo buteo* (buse variable)	habitat	060674	Tercafs	060675
	Oiseaux falconidés *Falco tinnunculus* (faucon crécerelle)	habitat	060674	Tercafs	060675
	Oiseaux apodides *Apus apus* (martinet)	habitat	060674	Tercafs	060675
	Oiseaux alaudinés *Alauda arvensis* (alouette des champs)	habiat	060674	Tercafs	060675
	Oiseaux corvidés *Pica pica* (pie)	habiat	060674	Tercafs	060675
	Oiseaux turdidés *Phoenicurus ochruros* (rouge-queue noir)	habiat	260373	Tercafs	260375
	Oiseaux sturnidés *Sturnus vulgaris* (étourneau)	habitat	060674	Tercafs	060675

Exploitation n °3.

Question de l'utilisateur : quel est l'indice de richesse relative des cases 1 ... *n*? L'indice de richesse relative utilisé ici peut être exprimé de deux façons différentes :

1° Il reprend simplement le nombre de paramètres (Zoologiques, Botaniques, Ecologiques,...) se trouvant dans les cases 1 ... *n* concernées par la question de l'utilisateur.

On peut limiter la question à une seule catégorie (par exemple les paramètres de la catégorie « Ecologie ») ou combiner plusieurs catégories (Botanique et Zoologie par exemple). Il s'agit donc d'une expression très simple définissant la richesse globale du territoire concerné par la question de l'utilisateur.

2° Une autre expression de l'indice de richesse relative choisi ici utilise aussi le nombre de paramètres rencontrés dans le territoire étudié, mais le compare au nombre total de paramètres existant dans la banque de données, appartenant à la même catégorie (par exemple la Zoologie), et exprime ce rapport en %. L'expression finale tient ainsi compte des paramètres présents dans un territoire par rapport à l'ensemble des paramètres du réseau. C'est donc bien une mesure de la richesse relative d'une parcelle.

Type de sortie : liste, visualisation sur imprimante ou sur table traçante (Exemple : voir annexe 3 a).

ANNEXE 3a

Coefficients de diversité et de valeur biologique

Catégorie n° 1

0101	0102	0103	0104	0105	0106	0107	0108	0109	0110
18,37% 0.1773	18,37% 0.1773	18,37% 0.1773	20,41% 0.1940	20,41% 0.1940	20,41% 0.1940	22,45% 0.2340	22,45% 0.2140	22,45% 0.2340	22,45% 0.2340
0201	0202	0203	0204	0205	0206	0207	0208	0209	0210
18,37% 0.1773	18,37% 0.1773	18,37% 0.1773	20,41% 0.1940	20,41% 0.1940	20,41% 0.1940	20,41% 0.2340	22,45% 0.2340	67,35% 0.6043	67,35% 0.6043

Question de l'utilisateur : quel est le coefficient d'occupation relative de 1 ... *n* paramètres dans l'ensemble du réseau? Le coefficient d'occupation relative d'un paramètre utilisé ici est le nombre de cases unitaires occupés par ce paramètre par rapport au nombre total de cases du réseau.

Type de sortie : liste.

Question de l'utilisateur : quel est le coefficient de valeur biologique de 1 ... *n* cases désignées? Le coefficient de valeur biologique d'une case utilisé ici est défini comme étant la somme des inverses des coefficients d'occupation des paramètres présents dans la case. Il tient donc compte du nombre de paramètres présents dans la case et de leur rareté relative dans l'ensemble du réseau. Il peut être pondéré par des facteurs extérieurs à l'écothèque par l'intermédiaire du fichier DICT.

Type de sortie : liste visualisation sur table traçante ou sur imprimante (voir annexe 3 b).

ANNEXE 3b

Visualisation des coefficients de valeur biologique

				+++++	++	++	++	+++++	+++
			+	++	+++++++ +++++++ +++++++ +++++++ +++++++ ++++	++	+++	+++	++

Exploitation n° 4.

Question de l'utilisateur : on demande la simulation d'une installation urbanistique dans 1 ... *n* cases désignées. Quelle est l'influence de cette installation sur les coefficients d'occupation des paramètres présents dans les cases 1 ... *n* désignées?

Type de sortie : liste en clair. La variation des coefficients d'occupation est exprimée en donnant le coefficient d'occupation ancien, le coefficient d'occupation nouveau, le pourcentage de variation (Exemple : voir annexe 4).

ANNEXE 4

Exploitation n° 4 (exemple)

Codes modifiés par la suppression des cases 101 102 103 104 201 202 203 204

N° de code	Libellé des codes		Coeff. d'occupation		% de variation
			ancien	nouveau	
1010503020110	Mammifères rongeurs muridés *Apodemus sylvaticus* (mulot)	habitat	94.00	86.00	— 8.50
1010503040110	Mammifères rongeurs muridés *Clethrionomys glareolus* (campagnol roux)	habitat	89.00	81.00	— 8.88
1020801010110	Oiseaux falconides *Buteo buteo* (buse variable)	habitat	33.00	25.00	— 24.13
1020801030110	Oiseaux falconidés *Falco tinnunculus* (faucon crécerelle)	habitat	33.00	25.00	— 24.13
1021301010110	Oiseaux apodidés *Apus apus* (martinet)	habitat	93.00	85.00	— 8.50
1021501010110	Oiseaux alaudinés *Alauda arvensis* (alouette des champs)	habitat	33.00	25.00	— 24.13
1021504020110	Oiseaux corvidés *Pica pica* (pie)	habitat	93.00	85.00	— 8.50

CONCLUSION

L'ensemble de ces exploitations, par l'utilisation de l'informatique, peut constituer un outil extrêmement précieux pour les études sur la gestion des espaces naturels et subnaturels. Les principaux avantages du système sont les suivants :

— les réponses aux questions des utilisateurs sont données en clair et non sous forme de codes ;

— la localisation géographique des paramètres est présentée de façon claire et pratique ;

— l'utilisation des coefficients proposés (coefficients d'occupation relative, de diversité, de valeur biologique) permet de décrire objectivement les caractéristiques du territoire concerné ; d'autres équations peuvent être expérimentées sans problème afin d'affiner l'évaluation biologique des sites ;

— la simulation de l'influence des implantations urbanistiques ou de tout autre altération permet d'inférer une politique de gestion en protégeant les zones écologiquement les plus intéressantes ;

— la terminologie utilisée permet un meilleur contact entre écologistes et urbanistes ;

— la procédure employée peut s'appliquer à l'étude de n'importe quel territoire naturel ou subnaturel. Elle s'inscrit dans le cadre des recommandations de l'Unesco (Documents de « International co-ordinating Council of the Programm on Man and the Biosphere », 1973) et constitue un exemple d'*écothèque régionale*.

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Juillet 1979 (*Communication reçue le 28 mars 1979*)

KAVALACYTHEREIS BRACONENSIS GEN. N., SP. N., A REMARKABLE NEW CYTHERACEAN OSTRACOD GENUS AND SPECIES FROM LAKE TANGANYIKA (ZAIRE)

by

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ABSTRACT

Kavalacythereis braconensis gen. n., sp. n., found in a bottom sample from Lake Tanganyika is described. The genus undoubtedly belongs to the Cytheracea, and is tentatively assigned to the family Cytherideidae. The presence of cytheracean genera of possible marine or brackish origin in the lake and its evolutionary implications are discussed.

RÉSUMÉ

Kavalacythereis braconensis gen. n., sp. n., trouvé dans un échantillon de fond du Lac Tanganyika est décrit. Le nouveau genre appartient indubitablement au Cytheracea et est attribué provisoirement à la famille des Cytherideidae. La présence dans le lac de genres cythéracés qui pourraient être d'origine marine ou saumâtre est discutée, ainsi que son implication évolutive.

I. INTRODUCTION

The ostracod fauna of Lake Tanganyika has been studied by Sars (1910), Lindroth (1956), Kiss (1959) and Rome (1962) but in spite of these important publications it remains insufficiently known. All the samples studied by Sars and most of those investigated by Rome were taken near the surface by the aid of fine meshed tow nets. Consequently, swimming forms were collected easily, but bottom dwellers, unable to swim, were only rarely caught by plankton net sampling.

Recently we found a bottom sample from the west-side of Lake Tanganyika in our collections. It yields a rich ostracod fauna and it contains a relatively large number of cytheracean genera. One of these genera is described herein.

II. ORIGIN OF THE MATERIAL

The material has been collected on February 2nd, 1947 by the « Exploration Hydrobiologique du Lac Tanganyika » (Leloup, 1949) in the Bracone Bay of Kavala Islet, at a depth of 12 m. Kavala is an islet near the west bank, at about 40 km N.E. of Kalemie (= Albertville), Zaire. The sample has been registered under n° 138. It is a dry sediment sample, containing a large amount of ostracod valves.

III. SYSTEMATICS

SUBCLASSIS OSTRACODA LATREILLE, 1806

ORDO PODOCOPIDA G. W. MUELLER, 1894
Superfamilia Cytheracea BAIRD, 1850
Familia Cytherideidae SARS, 1925
Genus *Kavalacythereis* gen. n.

Derivatio nominis : Kavala Islet in Lake Tanganyika.

Type-species : *Kavalacythereis braconensis* sp. n. (by monotypy).

Diagnosis : medium-sized valves with postero-dorsal and ventro-lateral hollow spines ; well developed selvage ; large anterior and small posterior vestibulum ; numerous compound marginal pore canals ; fulcral point present ; slightly modified merodont hinge with anti-slip bar ; striking sexual dimorphism.

Kavalacythereis braconensis sp. n.

(Pl. I, fig. 1-8 ; Pl. II, fig. 1-7)

Derivatio nominis : after the type-locality.

Type-locality : Bracone Bay, Lake Tanganyika.

Holotype : a male right valve (O.C. 1048).

Paratypes : 17 adult valves and 4 juvenile (A-1) valves (O.C. 1049-1059).

Description

The species has medium-sized, rather thickshelled and translucent valves. Dorsal margin straight, ventral margin slightly sinuous ; both margins tapering towards the posterior end ; the anterior margin abruptly rounded ; the posterior one evenly rounded ; cardinal angles absent ; the maximal height situated anteriorly, at the transition from the anterior to the dorsal margin ; the outline of the carapaces without prominences, fusiform in the males and wedge-shaped in the females ; the maximal width (without spines) situated in the middle for male carapaces and in the posterior area at about 4/5 of the length for the females.

The most prominent characteristics of the valves are the anterior flange and the postero-dorsal and ventro-lateral spines. The flange extends along the entire

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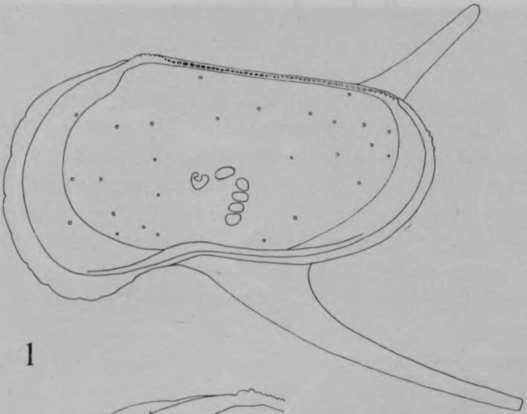
PLATE I

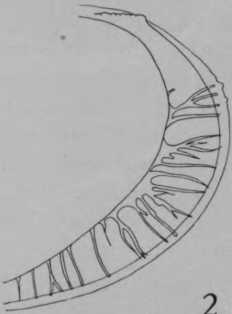
Kavalacythereis braconensis gen. n., sp. n., Bracone Bay, Kavala, Lake Tanganyika

Fig. 1 :	Right valve, male, internal view, holotype.
Fig. 2 :	Posterior marginal area, holotype.
Fig. 3 :	Anterior marginal area, holotype.
Fig. 4 :	Left valve, male, internal view, paratype.
Fig. 5 :	Left valve, male, dorsal view, paratype.
Fig. 6 :	Right valve, male, dorsal view, paratype.
Fig. 7 :	Left valve, female, dorsal view, paratype.
Fig. 8 :	Right valve, female, dorsal view, paratype.

PLATE I



1



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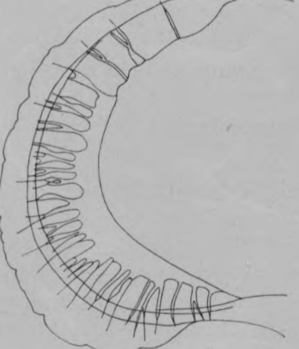

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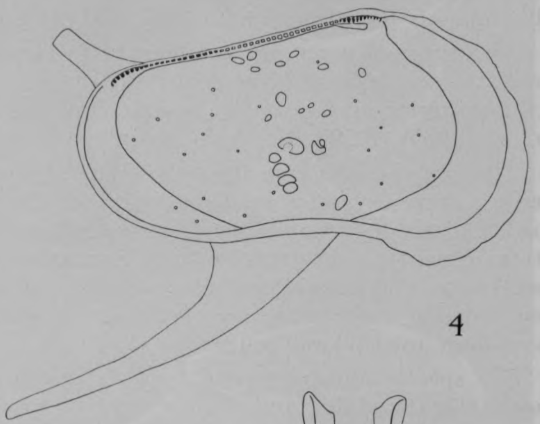

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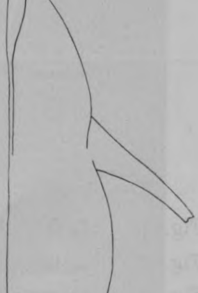


8

0.2 mm (Fig. 2, 3)

0.5 mm (Figs. 5-8)

0.5 mm (Fig. 1, 4)

anterior margin. It is raising from the valve surface at an angle of about 45°, and is slightly lobed at its distal margin. In dorsal view it appears as a large collar-like structure surrounding the anterior margin. Each valve bears two large, hollow spines. The ventro-lateral spine is the largest one. It has a broad, somewhat dorso-ventrally flattened base and bears a small proximal depression at the dorsal side. In dorsal view it is slightly curved, and in male specimens it extends beyond the posterior extremity. It is somewhat shorter in female specimens. The postero-dorsal spine is long and slender and only weakly curved. It is pointing obliquely upward, making an angle with the dorsal margin of about 120° in the males, and about 140° in the females. Female specimens are characterized by a pouch-like widening of the postero-dorsal area, with the postero-dorsal spine at the distal extremity of the pouch. This widening is most striking in dorsal view, giving the female carapace a wedge-shaped appearance, unlike the fusiform shape of the males. The valves are completely smooth.

The hinge in the left valve consists of an elongate crenulated anterior socket, with a large and smooth anti-slip bar, a crenulated antero-median groove, a crenulated postero-median bar and a crenulated elongate posterior socket. The right valve hinge is complementary to the left valve hinge, but lacks the anti-slip bar.

Two types of pores can be observed by means of the scanning electron microscope : the simple pores (type A of PURI and DICKAU, 1969) (Pl. II, fig. 7) occurring in the posterior area near the margin, and the sieve pores (type C of PURI and DICKAU, 1969) (Pl. II, fig. 5, 6) occurring elsewhere.

The inner lamella is moderately wide. It shows a well developed selvage. There is a large anterior and a small posterior vestibulum. The marginal pore canals are broad, indistinctly grouped together, and often bifurcated. The central muscle scar pattern consists of a vertical row of four suboval adductor scars and a U-shaped frontal scar. The anterior branch of the frontal scar sometimes separated from the stem, forming a separate scar ; between the frontal scar and the dorsal adductor scar a large oval fulcral point.

The species is characterized by a striking sexual dimorphism : the females are longer than the males, and show a large pouch-like widening of the valves in the postero-dorsal area.

PLATE II

Kavalacythereis braconensis gen. n., sp. n., Bracone Bay, Kavala, Lake Tanganyika

Fig. 1 : Left valve, male, lateral view, paratype ; stereo-pair, × 50.

Fig. 2 : Left valve, female, lateral view, paratype ; stereo-pair, × 50.

Fig. 3 : Right valve, male, lateral view, paratype ; × 50.

Fig. 4 : Left valve, female, postero-ventral view, paratype ; × 50.

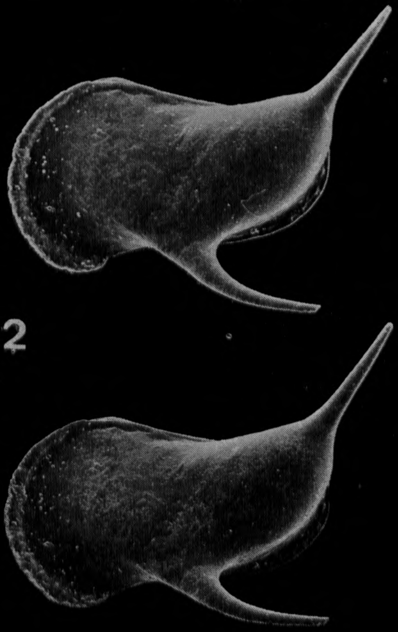
Fig. 5 : Sieve pore with seta, posterior area of a male right valve, paratype ; × 6600.

Fig. 6 : Sieve pore at the base of the ventro-lateral spine of the same male right valve as on fig. 5, paratype ; × 6600.

Fig. 7 : Normal pore near the posterior margin of the same male right valve as on fig. 5, paratype ; × 6600.

PLATE II


1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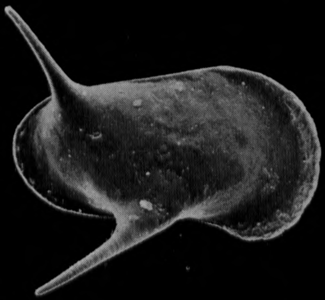
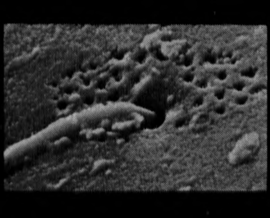
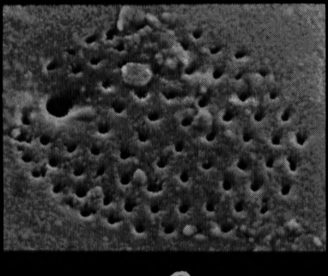
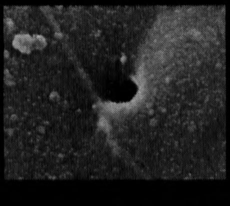

3


4


5


6


7

Dimensions. Holotype : length = 0.83 mm ; height = 0.43 mm
Paratypes

	N	M	SD	OR
L	17	0.84	0.031	0.79 — 0.89
H	17	0.46	0.023	0.42 — 0.50

where L = length ; H = height ; N = number of specimens ; M = mean ; SD = standard deviation and OR = observed range.

IV. DISCUSSION

A. The general morphology of our new genus, and in particular the muscle scar pattern with fulcral point, the hinge structure, the presence of sieve pores, the broad inner lamella with vestibulum and compound marginal pore canals and the rather thickshelled valves undoubtedly allow the assignment to the superfamilia Cytheracea BAIRD, 1850. Most representatives of this superfamily are living in marine or brackish environments. Some cytheracean ostracods, however, also occur in freshwater. Many of those belong to the family Limnocytheridae KLIE, 1938 and are characterized by ornamented or smooth valves, narrow inner lamella and poorly developed hinge. Even the unornamented genera as *Afrocythere* KLIE, 1935 and *Cytheridella* DADAY, 1905 still differ from our new genus by their hinge structure, by the morphology of the marginal zone, and by the absence of sieve pores. There are a few other cytheracean freshwater ostracod genera, such as *Cytherissa* SARS, 1925, practically confined to Lake Baikal, and characterized by weakly ornamented valves and a very narrow inner lamella. Some cytheraceans living in freshwater have a thalassogene origin, and can be considered as relicts (HARTMANN, 1975), namely *Pericythere* HARTMANN, 1957, *Hemicythere* SARS, 1925, *Cytherura* SARS, 1866 and *Leptocythere* SARS, 1925. None of these shows any resemblance to our new genus. The genus *Kavalacythereis* consequently does not show clear affinities to any known ostracod genus or even family, and its systematical position remains somewhat uncertain. Because of the hinge structure and the presence of a well developed fulcral point, the genus is tentatively assigned to the family Cytherideidae SARS, 1925.

B. The presence of a hitherto unknown cytheracean genus in Lake Tanganyika is not surprising in itself, but it gains in importance by the presence of other remarkable non-limnocytherid cytheracean genera in the lake. In 1959 KISS described the monotypic genus *Mesocythere* (non *Mesocythere* HARTMANN, 1956) from the northern part of Lake Tanganyika. It shows a remarkable resemblance to the genus *Perissocytheridea* STEPHENSON, 1938 for both soft part and valve characteristics. Species of the latter genus actually occur in marine to brackish environments of the Indo-pacific and W. Atlantic (HARTMANN, 1974). Another interesting genus from Lake Tanganyika is *Neocytheridea* ROME, 1962 (non *Neocytheridea* GREKOFF, 1953, non *Neocytheridea* RAJAGOPALAN, 1962). It has been described by ROME as a subgenus of the genus *Haplocytheridea* STEPHENSON, 1936, but HARTMANN and PURI (1974) raised it to the rank of genus. It belongs to the subfamily Cytherideinae SARS, 1925.

Representatives of this subfamily occur in marine to brackish environments, with exception of the genus *Cytherissa* SARS, 1925 and the poorly understood european genus *Romeis* SYWULA, 1970.

Apart from the species of the genera *Neocytheridea* ROME, *Mesocythere* KISS and *Kavalacythereis* gen. n., the studied sample yielded a number of species belonging to at least seven unknown and undescribed non-limnocytherid cytheracean genera, which will be studied later. Some of these definitely show affinities to known marine or brackish genera, such as *Loxoconcha* SARS, 1866, *Cyprideis* JONES, 1857 and *Leptocythere* SARS, 1928, but for the remaining four genera there is no resemblance to any known ostracod genus.

One can thus notice the presence of at least ten non-limnocytherid cytheracean genera in Lake Tanganyika. This is a rather unusual phenomenon since non-limnocytherid cytheraceans are practically confined to marine or brackish environments, and since no freshwater basin is known with such an elevated number of cytheracean genera. So far none of these genera ever has been found elsewhere, and they might be considered as endemics. Some restriction should be made for this statement because the East- and Central-African ostracod fauna is only partially known. Furthermore, these non-limnocytherid cytheraceans resemble their marine relatives in a general way, which allows them to be called freshwater ostracods with « thalassoid aspects ».

This « thalassoid aspect » is also found among the Tanganyikan prosobranch molluscs and is mostly determined by the general morphology, ornamentation and thickness of the shells. This has provoked vivid discussions on the origin of the fauna of the lake. It is not our intention to go into this matter or to open a new debate, but to draw the attention to this particularly interesting problem in relation to the ostracod fauna. The geological history of Lake Tanganyika has been characterized by a rather long period of isolation (1.5 to 6 million year after LANGDON BROOKS, 1950). Sublacustrine valleys occurring at a depth of about 550 m under the actual lake level (CAPART, 1949) are indications for important lake level changes during geological times.

C. To explain the presence of the higher mentioned cytheracean Ostracoda in Lake Tanganyika we can only formulate hypotheses.

1. These ostracods possibly originated either from a pre-Tanganyikan cytheracean ostracod fauna, and evolved independently during the isolation period, or otherwise they evolved from unknown Tanganyikan cytheraceans, not belonging to the limnocytherid stock. In both cases, the origin of the pre-Tanganyikan or Tanganyikan cytheraceans remains unexplained.

2. Another hypothesis assumes that during the long isolation period the lake has been subjected to an excessive evaporation, bringing about a higher ionic concentration and causing in a way a « salinity crisis ». Euryhaline, maybe brackish water cytheraceans may have been brought into the lake by passive migration. The surviving species evolved independently, in isolated conditions, becoming adapted to the new environment and giving rise to a particular endemic ostracod fauna. The large biotope diversity in Lake Tanganyika has surely favoured a rapid and diversifying evolution. This hypothesis at first sight seems to be far-fetched, but the presence of the genus *Mesocythere* KISS, resembling the genus *Perissocytheridea* to a very high degree, and the presence of genera resembling the genera *Loxoconcha*, *Leptocythere* and *Cyprideis*, all known to live in marine and brackish habitats, are

arguments in favour of it. Indeed, passive migration is not uncommon among Ostracoda, and it has been reported by several authors. Recently De Deckker (1977) pointed out that the dispersal of mytilocypridinid ostracods in Australia can be explained by the passive migration over long distances due to waterfowl migration. The dispersal of these ostracods (p. 285) « could come about by some of the continuously migrating waterfowl (often seen inhabiting brackish waters) carrying ostracods and ostracod eggs ». In the same way Sandberg (1964) established a correlation between the distribution of *Cyprideis*-species in the Americas and the migration patterns of birds. Klie (1939) even suggested passive migration by migratory birds as the means by which *Cyprideis torosa* has been introduced from the Mediterranean to Lake Turkana.

3. The whole problem can just as well be explained by accepting a convergent evolution. This frequently cited theory is based on the assumption that during the isolation period certain groups acquired thalassoid characters as a result of the rather high ionic concentration in the lake. This is not unlikely, but in our particular case the ancestors still should have been cytheraceans, and then again the origin of these ancestors would remain unexplained.

Whatever the explanation, the long isolation period of Lake Tanganyika, and perhaps its aberrant chemical composition in the past may have contributed to the particular characteristics of the ostracod fauna of the lake ; nevertheless Kufferath (1952) already stressed the point that the actual chemical composition gives no indication for the Tanganyikan endemism. He rather believed the long isolation period to be an important factor.

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A GENERIC REVISION OF THE FAMILY TYDEIDAE (ACARI : ACTINEDIDA)

I. INTRODUCTION, PARADIGMS AND GENERAL CLASSIFICATION (*)

by

Henri M. ANDRÉ (**)

SUMMARY

This paper analyzes the paradigms guiding the revision of the mites of the family Tydeidae. A general classification is advanced and seven new subfamilies are proposed (Australotydeinae, Pretydeinae, Pronematinae, Triophtydeinae, Tydaeolinae, Meyerellinae and Tydeinae).

INTRODUCTION

This generic revision deals with the mites of the family Tydeidae and is divided into four parts. The first part analyzes the paradigms guiding the revision and a general classification of the family is advanced. Organotaxy will be described in subsequent papers while the last part will deal with generic descriptions and present keys to stases, subfamilies and genera.

Two types of paradigms are proposed in this paper. A first type concerns acarology and refers to the work of Grandjean. It is both a synthesis and a translation of the main concepts advanced by the French acarologist. A second class of paradigms deals with systematics. An extensive review of the role and purpose of systematics is obviously beyond the field of this work. However, no classification may be advanced without some comments regarding the methodology used and its foundation.

A general classification is proposed. Seven subfamilies are distinguished. Subfamilial, generic and infrageneric criteria are debated. Lastly, a glossary of special terms and a list of abbreviations and symbols are presented as appendices.

A. PARADIGMS

1. *The nature and necessity of paradigms*

« No natural history can be interpreted in the absence of at least some implicit body of intertwined theoretical and methodological belief that permits selection,

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(*) This is a part of a thesis submitted to the Graduate School of the Oregon State University (Corvallis, OR 97331, U.S.A.) in partial fulfillment of the requirement of the degree of Master of Science. This work was achieved under Dr. G. W. Krantz, Professor of Entomology, to whom I am deeply indebted. This was read at a meeting of the society (17-III-1979).

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evaluation and criticism » (KUHN, 1970 : 16). In other words, as summarized by BERTALANFFY, science is not simply an accumulation of facts. Facts become knowledge only when they are incorporated into a conceptual system. This body of belief or this conceptual system, called a « paradigm » by Kuhn, may be considered as a basic feature of scientific activity. Kuhn analyzes some consequences of the absence of a paradigm :

- all the facts that could possibly pertain to the development of a given science are likely to seem equally relevant;
- early fact-gathering is a nearly random activity and is usually restricted to the wealth of data that is readily at hand;
- this sort of fact-collecting produces a morass.

This above description by KUHN is not unlike the situation that prevailed in acarology some years ago and that in fact is still appropriate in several taxa, including the family Tydeidae. Some examples from tydeid literature clearly illustrate KUHN's remarks. The ornamentation of the cuticle is generally considered to be as relevant as chaetotaxy in distinguishing genera. The chaetotactic formula generally given for leg I of the tydeid subfamily Pronematinae is wrong; only the eupathidia (which are very long) and an easily seen seta have been taken into account. However, a preliminary study of leg I of a variety of tydeids showed that, in addition, setae (u) were always present, even in the Pronematinae. Such inconsistencies produce great confusion. As pointed out by STRANDTMANN (1967), it is sometimes difficult to know to what genus a species belongs. As a case in point, the genus *Lorryia* as defined by BAKER (1965) illustrates several chaetotactic formulae, some of which are common to other genera.

Therefore, following a period of time devoted to accumulating materials, and after the first syntheses by BAKER (1965) and KUZNETZOV and LIVSHITZ (1973), I felt it was time to review the Tydeidae. I decided that such a revision must be based on elaborate morphological observations; since any description must be partial, the typical natural history study often omits just those details that later scientists find to be sources of important information (KUHN, 1970 : 16). In addition, it was decided that such a revision must rest on established paradigms in order to avoid an unmethodical and fruitless approach. Before defining these paradigms, it should be emphasized that a paradigm is not a rule and that scientists can agree in their *identification* of a paradigm without agreeing on, or even attempting to produce, a full *interpretation* or *rationalization* of it. « Lack of a standard interpretation or of an agreed reduction to rules will not prevent a paradigm from guiding research » (KUHN, 1970 : 44).

2. *A fundamental paradigm*

Evolution cannot be considered as a random phenomenon; on the contrary, evolution is supposed to be governed by laws and to follow a strategy. This point of view is well expressed by the famous SIMON's fable of the two watchmakers (1965). Briefly, two watchmakers, Hora and Tempus, make watches consisting of a thousand parts each. Hora assembles his watches part by part whereas Tempus puts together sub-assemblies of ten parts each, assembling these into a larger sub-assembly of a hundred units; ten of these larger sub-assemblies make the whole watch. At each disturbance, the watch Hora tries to assemble falls to pieces and he has to start over again. On the contrary, if there is a disturbance, Tempus has to repeat at most nine assembling operations, and possibly none at all. At a ratio of one disturbance in a hundred operations, Hora will take 4000 times longer to assemble a watch than will Tempus. This fable illustrates the properties of hierarchical systems. These are the systems that have time to advance and are characterized by incomparably greater stability and resilience. Evolution follows such a strategy (KOESTLER, 1972).

The general properties of an element of such a hierarchy — called holon by Koestler or integron by JACOB (1970) — are closely developed by KOESTLER (1967). Some of them are fundamental and deserve some comment here.

« 1. Functional holons are governed by fixed sets of rules and display more or less flexible strategies.

2. The rules — referred to as the system's *canon* — determine its invariant properties, its structures, configuration and/or functional pattern.

3. While the canon defines the permissible steps in the holon's activity, the strategic selection of the actual step among permissible choices is guided by the contingencies of the environment.

4. The canon determines the rules of the game, strategy decides the course of the game.

5. The evolutionary process plays variations on a limited number of canonical themes. The constraints imposed by the evolutionary canon are illustrated by the phenomena of homology, homeoplasy, parallelism, convergence and the *loi du balancement* » (KOESTLER, 1967).

The goal of Grandjean was no doubt to try to understand the *canons*, the laws which guide the evolution of mites. In logic, such canons are expressed in terms of *relations*. A relation between sets A_1, A_2, ... A_n, is a subset of the cartesian product $A_1 \times A_2 \times \ldots \times A_n$:

$$R_{1 \leq i \leq n}\ (A_i) \subseteq X_{1 \leq i \leq n}\ A_i$$

A good example is offered by genital and aggenital setae in Tydeidae. Set A_1 includes six aggenital elements and A_2 comprises six genital elements. Thus, the cartesian product involves 49 possible combinations, among which only a few really exist. Consequently, there is a relation between these two sets which could be expressed as a law. The work of GRANDJEAN contains numerous observations which lead to formulating such rules or canons.

The purpose of this work is to gain an understanding of the rules governing the evolutionary behavior and strategies of the holon called Tydeidae. Such an undertaking is of course impossible without the help of an adequate methodology, and without having recourse to some of the concepts already expressed by Grandjean.

3. *Methodology*

Methodology in an acarological study essentially consists of acute observation of the object under study in three-dimensional view, and its eventual description by graphic processes or by formulae. The iconographic description of a mite should be devised as a drafting as well as a drawing. « Orthographic projections are views of an object taken at right angles to the object and arranged in specific relative positions on the drawing » (BETHUNE, 1977). Surely, it is not necessary to describe a mite in such a way. However, from the six possible orthogonal views of an object (front, top, bottom, right side, left side and rear views), three are usually used : the top view (i.e. a dorsal view), the bottom view (i.e. a ventral view), and a lateral view. These views have to be orthogonal, which means that, in the case of a dorsal view, the symmetry plane must be vertical or practically speaking, that a pair of homologous organs must stay in the same horizontal plane. Even if the three orthogonal views are not reproduced in the published description, the study of a mite from these three points of view (and sometimes from intermediate points of view) remains the only way to understand a mite as a three-dimensional object.

These three views are useful for understanding the morphology of the body, but the study of appendages is a bit more complex. In this case, one has to distinguish, in addition to the dorsal and ventral views, the two side views. The right and left lateral views are not homologous in that a leg is divided by a pseudosymmetrical plane and the prime face (′) may be distinguish from the second face (″). The prime side is the anterior aspect of the appendage when it is perpendicular to the body. A given aspect of an appendage or part of an appendage will also be spoken of as the paraxial (π) or the antiaxial (α) face depending on whether the side is towards the body or not. Lastly, as a segment or a leg may be considered as a cylinder, they may be studied in end view. This allows one to know exactly where the setal insertions lie. Indeed, it may be difficult to decide whether a seta is antiaxial or paraxial in lateral view. Moreover the end view is sometimes the only way to know how many setae arise from the end of minute terminal segments, such as the palp tarsus.

It goes without saying that a description of the type described above requires good examination techniques. The observation of mites in cavity slides has been described previously (Grandjean, 1949; Travé, 1965; van der Hammen, 1972; Coineau, 1974). As emphasized by Coineau (1974), this is the best method for morphological studies with a microscope. The medium used is lactic acid, which provides the advantages of low refraction index, low volatily, reasonably good preservation qualities and miscibility in water in any proportion. Permanent slides present many disadvantages. Specimens flattened in permanent mounts are often impossible to use in a critical morphological study. It is difficult or even impossible to understand a three-dimensional object when it is observed only from one point of view. For example, the paraproctal suckers of Tydeidae, which are sometimes very well developed, have almost always been « forgotten » because they are difficult to discern in dorsal or ventral views. Furthermore, an ideal orientation for making valid comparisons is rarely obtained in a permanent mount. In fact, getting a good orientation even in a cavity slide is sometimes difficult and it often takes more time to put the specimen in the right position than to draw it. Some details are visible only from a very special angle; e.g. the famulus of *Pseudotydeus perplexus*. Lastly, some details are difficult to see in permanent mounts even when the orientation is satisfactory. For example, the palp solenidion of genus *Meyerella* could not be discerned in a permanent slide, so that it was necessary to transfer the specimen to a cavity slide. The refraction index of the medium is very important here, especially when working at the resolution limit of the microscope. Some eupathidia also are difficult to see in permanent slides, often because of poor orientation and the transparency of the structure. Lastly, dissecting a specimen is sometimes the only one way to check a feature. For instance, the palp is difficult to study in end view on a whole specimen because other appendages tend to confuse the view.

Working with a light microscope was found to present some difficulties during the course of this study. For instance, it often was difficult to verify the presence of vestigial setae with a light system. A better understanding may have been gained through use of the scanning microscope. This method was not used here for several reasons, the main one being that such a study would have to be considered secondary. Scanning microscopy is a fairly exotic technique which is not generally used for « routine » identification. For this reason, every observation reported in this work has been based on study with a light microscope equipped with phase contrast.

4. *Some fundamental paradigms of Grandjean*

— *Stase and ontogeny.* The concept of stase is fundamental in the work of GRANDJEAN (1938*c*, 1951, 1957, 1959). It differs in basic ways from the other ontogenic concepts, such as that of « instar », for instance. The terms « instar » and « stadium » refer to an animal or to a period of its life between two successive moltings (JONES, 1978). The difference between these terms is just a matter of convention. A problem arises because words are discrete units used to describe a continuum (1), the life of an animal.

A stase is one of the successive forms through which an animal passes, these forms being different from one another by the criterion of « all or none ». The change in character is emphasized, not the change of skin. In other words, a stase is an animal at any level of its ontogeny. As a consequence, a stase is always an instar, but not the reverse. Logically, stase is a proprer subset of the set « instar ».

There exists seven forms through which a mite passes (2) : the egg, prelarva, larva, protonymph, deutonymph, tritonymph and adult. By definition, all but the egg are considered as stases (3). They are idionymic, which is another fundamental difference between the concepts of stase and instar.

Two particular stases were emphasized by GRANDJEAN. Elattostasis (1957) is a stase whose mouthparts are reduced in such a way that the animal is unable to eat. Calyptostasis (1951) differs from elattostasis in that calyptostatic forms lose the appendages or at least their use, particularly the legs (4). Calyptostasis is quite common in the Insecta. A typical case is the chrysalid of a butterfly.

— *The theory of « l'évolution selon l'âge ».* Stases, therefore, are steps through ontogeny characterized by features which are discrete units, by characters of « all

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(1) This continuum is sensed as a series of discrete units at a particular time resolution level : a butterfly is a nymph on one day, and an imago the next. But if a finer resolution level is chosen, the development is of course continuous.

(2) In « mites », I include only the Actinotrichida or Acariformes. The stases found among the Parasitiformes are not homologous with the stases of Actinotrichida. In other words, a larva of Gamasida does not belong to the same ontogenic level as a larva of Tydeidae (ATHIAS-HENRIOT, 1975).

(3) GRANDJEAN excluded the egg as a stase in 1957 (Remark 11) and in 1970. Most prelarva are calyptostatic and have no chaetotaxy because they have lost their setae. An egg has no setae either, not because the egg has lost its setae but rather because chaetotaxy does not exist at this level (otherwise, it should be considered as a special calyptostasis). It is thus impossible to make any real comparison between an egg and the other forms; therefore, the egg is not considered as a stase. As pointed out by GRANDJEAN (1957), a problem arises because the term « absence » is ambiguous. Later, « absence » will be shown to mean disappearance following presence.

(4) Once again, words are discrete units and some particular cases fall somewhere « between » calypto- and elattostasis.

or none ». GRANDJEAN was interested in the relation between ontogeny (defined as a succession of steps) and phylogeny, and advanced the idea that *each level of development has its own phylogeny.* In other words, an animal has as many phylogenes as stases, and it is pointless to speak about THE phylogeny of a species. This is nothing less than a scientific revolution sensu KUHN (1970) and upsets many existing interpretations. GRANDJEAN's stase concept is closely explained in two detailed papers (1951, 1957) (5); and is summarized by VAN DER HAMMEN (1964) and COINEAU (1974).

One of the features of mites which intrigued Grandjean and led him to the theory of the « evolution selon l'âge » is the occurrence of calyptostasis at any level of mite ontogeny. Calyptostatic inhibition occurs once or several times throughout the ontogeny, seemingly at random, between homeo- and heteromorphic stases. This special and very advanced type of evolution seems thus a stochastic process whose true meaning is not yet understood. The only consistent explanation for calyptostasis is that this very regressive state is a stase which followed its own evolution; it is not an intercalary or added state allowing a metamorphosis. Thus, the chrysalid is not a transition state between the caterpillar and the butterfly. There are two (and not one) « metamorphoses » : one from the caterpillar into the chrysalid and a second from the chrysalid into the adult. The old concept of a transition state between the caterpillar and the butterfly loses credence when one observes calyptostasis occuring between homeomorphic mite stases. This type of regression, or more precisely this type of inhibition (6), seems rather special and is called a « deficiency level » by GRANDJEAN (1951).

It must be mentioned that independent phylogeny in a given stase describes a possibility, not an obligation. In other words, the phylogeny of a stase may be quite divergent from that of any other stase or the different phylogenies may be parallel and the stases homeomorphic. In any case, the conclusions will be the same, as seen below.

— *Ontogeny and phylogenies.* The principle that « ontogeny recapitulates phylogeny » is a famous phylogenetic concept. Some biologists agree with it, some others do not. The following examples point out that the concepts of independent stase and of ontogenic recapitulation are essentially different.

Let P be a primitive character, i.e. a character which through phylogenic time *T*, precedes a derived or secondary character, S. There is no intermediate step between P and S and they are exclusive. What happens through ontogenic time *t*? A priori, these are three possibilities : P precedes S or P comes after S, or thirdly either P or S may be present through the entire ontogeny. The three situations are found among tydeid mites and are illustrated by ontophylogenic diagrams (GRANDJEAN, 1957) (figure 1).

Diagram A refers to the tarsal setae (*it*) which are sometimes eupathidial. The eupathidial character is considered to be the most primitive state, while the normal setae is the derived state; the absence of the setae is a character which is still more advanced. These three states are plotted against ontogenic time, *t*, and the phylogenic time, *T*. Lines may be drawn to separate the three states. Plotting of this data results in what GRANDJEAN (1951) called an *ascendent harmony* or, since it is

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(5) These ideas had already been expressed in earlier papers. However, these two references are essential to understanding.

(6) COINEAU (1974 : 110) prefers the term « inhibition » rather than « regression ».

a regression along time *T*, a retroprogression. This means that, through ontogeny, the character S precedes the character P or, briefly, that the larva is « more advanced » than the adult in this respect. This example negates the recapitulation theory of earlier authors. Diagram B refers to another 3-state character. P is represented by

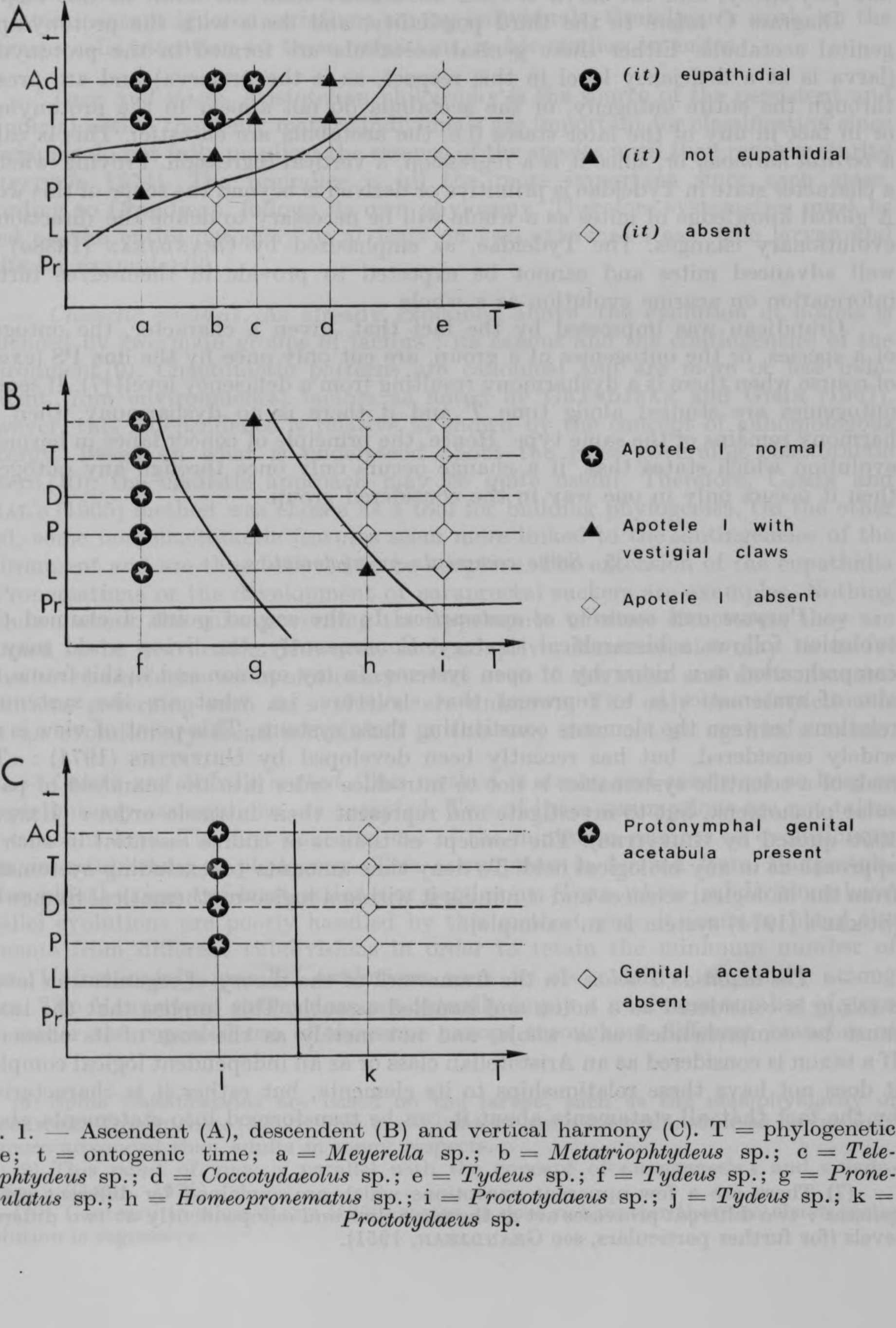

Fig. 1. — Ascendent (A), descendent (B) and vertical harmony (C). T = phylogenetic time; t = ontogenic time; a = *Meyerella* sp.; b = *Metatriophtydeus* sp.; c = *Teletriophtydeus* sp.; d = *Coccotydaeolus* sp.; e = *Tydeus* sp.; f = *Tydeus* sp.; g = *Pronecupulatus* sp.; h = *Homeopronematus* sp.; i = *Proctotydaeus* sp.; j = *Tydeus* sp.; k = *Proctotydaeus* sp.

the presence of apotele I, the derived state is the presence of vestigial claws, and the very advanced state is the complete disappearance of the apotele. The resulting diagram is the reverse of the previous one, in that the separating lines are descendent. This is a *descendent harmony* or, since it is a regression along time *T*, a retroregression. The character P precedes the character S both through ontogeny and phylogeny, and the larva is « less advanced » than the adult in this respect.

Diagram C refers to the third possibility, and deals with the protonymphal genital acetabula. Either these genital acetabula are formed in the protonymph (larva is at a deficiency level in this respect, as is the prelarva) and are present through the entire ontogeny, or the acetabula do not appear in the protonymph, or in fact in any of the later stases (i.e. the acetabula are eustatic). This is called a *vertical harmony* or, since it is a regression, a vertical regression. Proving whether a character state in Tydeidae is primitive or derived is beyond the scope of this work. A global knowledge of mites as a whole will be necessary to define the direction of evolutionary changes. The Tydeidae, as emphasized by GRANDJEAN (1938*a*) are well advanced mites and cannot be expected to provide in themselves further information on acarine evolution as a whole.

Grandjean was impressed by the fact that, given a character, the ontogeny of a species, or the ontogenies of a group, are cut only once by the line PS (except of course when there is a dysharmony resulting from a deficiency level) (7). If several ontogenies are studied along time *T* and if there is no dysharmony, then the harmony remains of the same type. Hence, the principle of concordance in harmonic evolution which states that, if a change occurs only once through any ontogeny, then it occurs only in one way in the considered group.

5. *Some comments on systematics*

— *Purpose and meaning of systematics.* In the second point, I claimed that evolution follows a hierarchical strategy. Consequently, the living world may be comprehended as a hierarchy of open systems. In my opinion and in this frame, the aim of systematics is to represent that structure, i.e. what are the systematic relations between the elements constituting these systems. This point of view is not widely considered, but has recently been developed by GRIFFITHS (1974) : « The task of a scientific systematics is not to introduce order into the manifold of particular phenomena, but to investigate and represent their intrinsic order » (HENNIG, 1950 quoted by GRIFFITHS). The concept of time is of course essential in such an approach as in any biological field. To deny time amounts to excluding systematics from the biological sciences and confining it within a logico-mathematical framework (SOKAL's (1974) system is an example).

— *The taxon as a holon.* In the framework of the theory of organization levels, a taxon is considered as a holon and handled as such. This implies that the taxon must be comprehended as a whole, and not merely as the sum of its elements. If a taxon is considered as an Aristotelian class or as an independent logical complex, it does not have these relationships to its elements, but rather it is characterized by the fact that all statements about it can be transformed into statements about

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(7) There are a few apparent exceptions which are explained by different orthogeneses : two different processes act at the same time and independently at two different levels (for further particulars, see GRANDJEAN, 1951).

its elements (Carnap, 1967 : 9). A class is therefore defined as « the extension of property » (ibidem : 57). The latter interpretation cannot be accepted here. Later, in this work, a species will be described by the following statement « ♂ : 4 (*ge*) (occurrence 100 %) — ♀ : 3 (*ge*) (occurrence : 17,5 %) ». It is obvious that such a statement is irrelevant for any particular individual, since it refers to the species as a system and not as a class sharing common characteristics with its constituents. The latter concept ignores variations among individuals. Grandjean's work, on the contrary, calls attention to these variations in his studies on mites.

— *Taxa and stases.* Aristotelian philosophy is the source of the persistent and prejudicial notion that only mature individuals are important for classification since individuals do not fully manifest the essence of the species until they reach maturity (Griffiths, 1974). The prejudice is all the more important since each stase, according to Grandjean, follows its own phylogeny. Therefore systematics must be based on the entire ontogeny or at least on two extremes stases (the larvae and adults for example) (8).

— *Cladistic analysis.* As already explained above, the evolution of holons is influenced by two main groups of factors : its canons and the contingencies of the environment (9). Chaetotactic patterns are canonical and are more or less independent from environmental factors as noted by Grandjean and Gisin (1967). However, this independence is relative as shown by the concept of anhomologous tautergy. Based on what is understood about the rules governing chaetotactic pattern (10), the cladistic approach may be quite useful. Therefore, Camin and Sokal's (1965) method was chosen as a tool for building phylogenies. On the other hand, some non-chaetotactic features seem more linked to the contingencies of the environment and are thus believed to be adaptive. The extension of the eupathidia in Pronematinae or the development of paraproctal suckers are examples. Nothing is known about the rules governing the appearance of these structures; they are assumed to be irreversible. However, such adaptive characteristics may be useful to better characterize an evolutionary trend even if the rules and environmental conditions governing such an evolution are unknown. The only one restriction is that an evolutionary trend established in this way may not go against a canon.

— *Camin and Sokal's method.* This method is strong and consistent as long as the preliminary assumptions are accepted. Two of these assumptions are not taken into account here. The first concerns use of the minimum number of evolutionary steps in establishing a phylogeny. This assumption is derived from Maupertuis' philosophical axiom « of least action » or parsimony. Taxa whose subdivisions have parallel evolutions are poorly handled by this method since it tends to blend the elements from different subdivisions in order to retain the minimum number of steps. Unfortunately, parallel evolutions seem to occur fairly frequently among mites. The Maupertuis' axiom does not actually imply a minimum number of steps but rather the repeated use of the same canons throughout different branches of

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(8) Some classifications are based on the larvae, such as the nepophylogeny of Vercammen-Grandjean (1969). This is relevant to some extent, insofar as larvae may be more advanced than adults in many respects.

(9) This point of view is parallel with the concept of « anagenesis » and « cladogenesis » (Gama, 1971).

(10) Contrary to what Mayr (1969) states, it does not matter that the chaetotactic evolution is regressive.

a cladogram. The problem above arises partly because the characters used are supposedly equal. Yet to each systematic level belongs a special set of characters and this exactly describes the theory of organization levels. The study of the canons allows *a posteriori* weighting of these characters. Therefore, Camin and Sokal's method was used after having imposed some priority among the characters used. Nevertheless, this method remains debatable, not because of its lack of consistency, but because it depends too much on the number of characters used and the number of species available. However, the method is heuristic in that it provides ideas about gaps between the different O.T.U.'s (Operational Taxonomic Unit).

— *Classification.* As noted by MAYR (1974), the cladistic analysis does not necessarily imply a cladistic classification. The reconstitution of a phylogeny is a deductive process and a cladogram is supposed to call up the story of a group. Such a process is therefore susceptible to falsification, according to Popperian philosophy (KITTS, 1974). This is not the case of classification which is essentially a matter of convention. A genus is separated from other taxa of the same rank by a decided gap (MAYR, 1969), but no one has ever defined the width of such a gap. Consistency within a group is the only rule. The problem arises from the fact that words are discrete units and are used to describe continuous phenomena.

B. GENERAL CLASSIFICATION

1. *The subfamilial level*

The solenidiotaxy of the Tydeidae is greatly reduced and consists of only five solenidia : palpal ω, ω I, ω II, φ I, and φ II. Clearly, only very strong solenidia have persisted and these apparently are eustatic. Solenidion φ II exists only in *Meyerella* and always is recessed; φ I is more common, but sometimes is also recessed; ω II is seldom absent and ω I is always present. The strength of these solenidia and their special nature suggests that they can be a useful criterion for distinguishing the tydeid subfamilies (11).

Lyrifissures number four pairs in Tydeidae except in *Tydeus* and some other genera. The canons regulating lyrifissures are not well known, but they seem eustatic. In any case, their presence is certainly not stochastic, and their disappearance within the family is somewhat surprising. Absence of lyrifissures (*ip*) separates *Tydeus* and other genera from the rest of the Tydeidae.

Genital acetabula are eustatic. The tritonymphal acetabular pair is missing in all the Tydeidae. The regression continues in some genera which lose one or two pairs of genital acetabula.

The disappearance of apotele I or at least its regression and the concomitant elongation of the adjacent eupathidia seems to be another subfamilial criterion. While this phenomenon has occured in several families (even among Oribatida), it is not common. Certainly it is doubtful that it occurs more than once among the tydeid subfamilies.

The shape of the dehiscence line of the prodorsum is another useful subfamilial character even if some intermediate cases exist between the procurved and the recurved types. The number of eyes could be another good criterion but further

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(11) An exception will be made for ω II which disappears only in a few specimens for which it would be premature to create a subfamily.

information is necessary on this point. There are three eyes in *Meyerella*, *Apotriophtydeus*, and *Metatriophtydeus*, and only two in *Tydeus* and *Lasiotydeus*. No eyes were seen in *Homeopronematus*, *Coccotydaeolus*, *Tydaeolus*...

Some other chaetotactic characters are of interest. A case in point is the coxisternal or epimeral chaetotaxy. The epimeral paleotaxy is (3-1-4-3) and has been seen only in *Tydaeolinae*, and in *Australotydeus*. Either seta *3d* drops out (*Meyerella*, *Metatriophtydeus*...) or *4c* is absent (*Tydeus*). Seta *l2* is especially interesting in that it has been observed only in the genus *Australotydeus*. It is not only absent in other Tydeidae, but also in the tydeoid family Ereynetidae and apparently in the Paratydeidae. It is thus a special and primitive character, the presence of which makes it necessary to classify *Australotydeus* apart from the other tydeid genera. Other characters may be of value in better describing subfamilies, but what is important is the set of criteria selected above and expressed in figure 2. These criteria distinguish seven subfamilies, all of which are new since no subfamilies were created in previous revisions. These are the Australotydeinae, Meyerellinae, Triophtydeinae, Tydeinae, Pretydeinae, Pronematinae and Tydaeolinae.

An interpretation of the general phylogeny (12) of Tydeidae as an amalgam of these subfamilies is proposed in figure 2. The number of evolutionary steps *sensu* Gisin (1967) (13) is expressed in the ordinate. This scale rests only on organotactic characters, such as phanerotaxy and idiotaxy, i.e. on discrete or discontinuous characters (Grandjean, 1951) as well as on apotele I. Some characters of an adaptative nature could be introduced in a third dimension but such characters are more difficult to quantify even arbitrarily. Of course, the selected scale is also arbitrary and the resulting pattern is all the more relative.

Subfamilies are represented by terminal leaf-like expansions. Each expansion has a lower and an upper limit which respectively represents the number of evolutionary steps of the less and the more advanced species in respect to organotaxy. The width of the expansion was determined in such a manner that its area is more or less proportional to the number of species described in the subfamily (14). Since the subfamilies are well advanced in their own directions on the basis of the criteria used, it is difficult to determine how they may have begun their own evolution. It is the reason why the origins of the different subfamilies are expressed as free entities in the diagram. The diagram also has « contour » lines which delimit the presence of certain characters used in defining the subfamilies.

The different subfamilies may be described as follows :

Australotydeinae n. subfam.

Prodorsum recurved (15); setae (*l2*) present on the opisthosoma (unique); four pairs of lyrifissures; two pairs of genital acetabula, eugenitals present at least in ♂, longitudinal progenital aperture in ♂, progenital depression in nymphs, cis-acetabular

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(12) In this particular case, it is not too wrong to speak about the general phylogeny of Tydeidae as long as phylogenies of different stases are in harmony. Of course, the prelarva is calyptostatic.

(13) Contrary to the opinion of Griffiths (1974), it is not immaterial as to whether one uses time or evolutionary steps as the ordinate. The resulting diagrams are somewhat different due to different points of view in data analysis.

(14) Only the species mentioned in the revisions of Baker and Kuznetzov, and those amply described before or subsequently, are taken into account here.

(15) This does not refer to the shape of the prodorsum but to the shape of the dehiscence line and the location of the prodorsal setae as explained in part II.

area absent in nymphs; epimeral formula (3-1-4-3) in the adults, coxal organ present; femora IV fused, setae *tr* I, II and III present in adults, two solenidia on the legs (ω I, ω II), five eupathidia on tarsus I, none on other segments; terminal eupathidium at the tip of the palp tarsus seemingly double.

Paraproctal suckers are well developed in the only one species known.

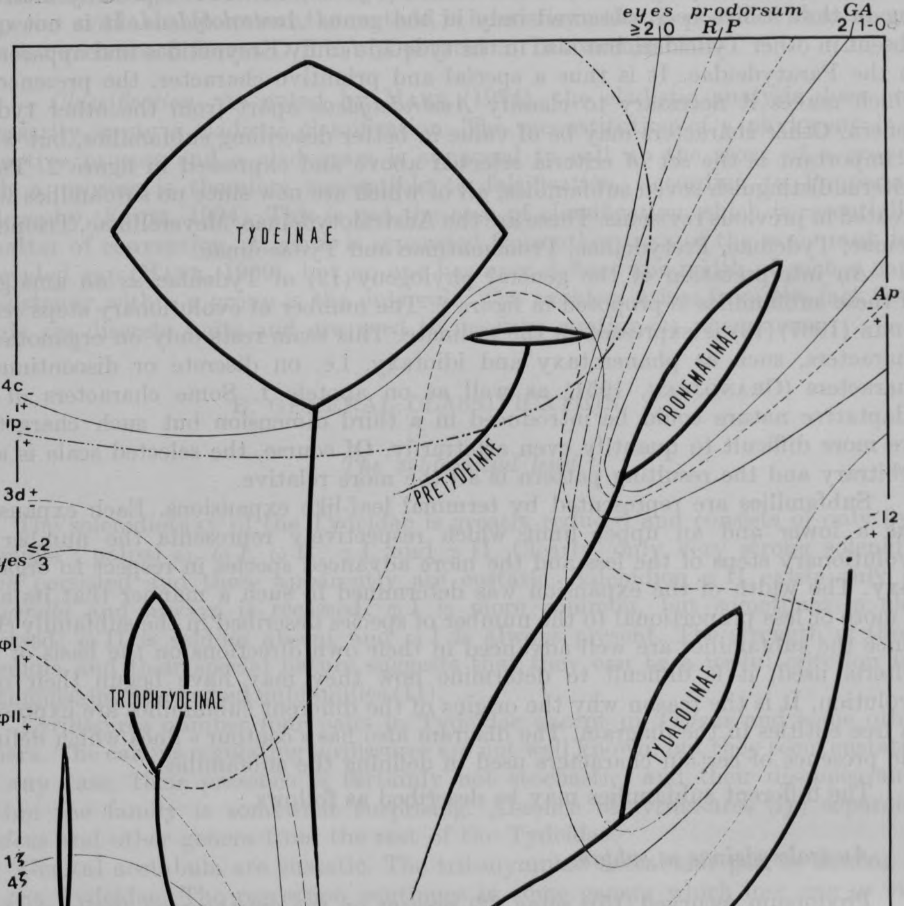

Fig. 2. — Hypothetical phylogeny of subfamilies of Tydeidae. « Contour » lines delimit the occurrence of certain characters used in defining the subfamilies (special abbreviations : *GA* : genital acetabula; *Ap* : apotele I; *R* : recurved; *P* : procurved; 1ζ and 4ζ refer to the palp eupathidia; + : present; — : absent [or reduced when apotele I is concerned]).

Meyerellinae n. subfam.

Prodorsum recurved with three eyes; four pairs of lyrifissures; two pairs of genital acetabula, eugenitals present in ♀ and ♂, longitudinal progenital aperture; progenital groove in nymphs with cis-acetabulal area; epimeral formula (3-1-3-3) in adults, femur IV divided, four solenidia on the legs (ω I, ω II, φ I, φ II) (unique), one to eight eupathidia on tarsus I, one on tarsus II and sometimes another on tibia I; four distinct eupathidia at the tip of the palp tarsus in *Meyerella*, multiple eupathidium in *Pseudotriophtydeus*.

The Meyerellinae is the only subfamily with setae *tr* IV but their appearance is delayed until the tritonymphal stase in *Meyerella*; their total disappearance is observed in *Pseudotriophtydeus*.

Pretydeinae n. subfam.

Prodorsum recurved; opisthosoma with three pairs of lyrifissures (*ip* absent); two pairs of genital acetabula, eugenitals present only in ♂, longitudinal progenital aperture in ♂, recumbent-H shaped in ♀, no cis-acetabulal area in nymphs but a sign of the anterior apex of the progenital chamber; epimeral formula (3-1-4-2) in adults, coxal organ present; femora IV undivided; leg chaetotaxy reduced; genua II, III and IV nude, *tr* I, II and III present in adults; three solenidia on the legs, ω I, ω II and φ I (the latter absent in one case), slightly recessed particularly φ I; at the most five eupathidia on tarsus I, eupathidia absent on the other leg segments; simple or double anabasis; multiple eupathidium at the tip of the palp tarsus, with three terminal tines.

The anagenesis of the Pretydeinae is characterized by the appearance of the empodial claw as in some Tydeinae.

Pronematinae n. subfam.

Prodorsum procurved, no eyes at least in one genus, sensilla may be clublike; four pairs of lyrifissures; two to zero pairs of genital acetabula, no eugenitals or genitals, progenital aperture varying from a five-branches shape to a transverse split, cis-acetabulal area in nymphs absent or very reduced; paraproctal suckers often well developed; epimeral formula (3-1-4-2) in adults; apotele I with vestigial claws or absent; pretarsi II, III and IV with strong condylophores; femur IV divided or undivided; *tr* III always present in adults and *tr* IV always lacking; three solenidia on the legs (ω I, ω II and φ I); generally, five eupathidia on tarsus I, very long; in a few cases, an eupathidial seta on tarsus II; double anabasis; terminal eupathidium of the palp tarsus seemingly double; only one seta on the palp tibia.

The regression of apotele I could be interpreted as being recent. However, femur IV is still divided in several pronematine genera and seta *p′* II of *Parapronematus* has retained the eupathidial condition. This indicates that the subfamily began its « palpian evolution » pretty early. The different location of the progenital aperture in ♂ and ♀, the structure of genitalia and the presence of a dorsal excressence on femur IV suggest that true mating may occur among pronematinae. Direct sperm transfer is highly advanced strategy when compared to reproduction by means of spermatophores as has been observed in Tydeinae (SCHUSTER, 1970). Such a difference would be quite important from an evolutionary standpoint.

Several pronematine species have been taken on insects, and certain adaptive characters suggest this type of relationship; i.e. slender pretarsi, strong condylophores, paraproctal suckers, and pulvillus.

Triophtydeinae n. subfam.

Prodorsum recurved with three eyes; four pairs of lyrifissures; two pairs of genital acetabula, eugenitals in ♀ and ♂, progenital aperture longitudinal in ♂ and recumbent-H shaped in ♀, cis-acetabulal area present in nymphs; epimeral formula (3-1-3-3) in adults; femur IV generally divided; (*it*) present on tarsus I in adults but not always eupathidial, three other pairs of eupathidia on tarsus I; often with other eupathidia on tibia I, and on tarsi II, III and IV; simple anabasis; two solenidia on the legs (ω I and ω II); triple eupathidium at the tip of the palptarsus.

The subfamily is characterized by its special leg chaetotactic regression as explained in part III. It is noteworthy that most members of the Triophtydeinae are found in the Arctic or Antarctic realms or in particularly uncogenial environments such the cortical medium on trees.

Tydaeolinae n. subfam.

Prodorsum procurved, no eyes, sensillum sometimes clublike; four lyrifissures; two pairs of genital acetabula, eugenitals present only in ♂; progenital aperture longitudinal in ♂, recumbent-H shaped in ♀, cis-acetabulal area absent in nymphs; epimeral formula (3-1-4-3) in adults; leg chaetotaxy rich; (*it*) present but not eupathidial in adults, at most, five euphatidia on tarsus I, eupathidia absent on other segments, femur IV undivided; setae *tr* I, II and III present in adults; three solenidia on legs (ω I, ω II and φ I); double anabasis; trifurcated eupathidium at the end of the palp tarsus.

As in the Tydeinae, the subfamily is cosmopolitan and occurs in diverse habitats such as soil, plants and birds. The paraproctal lips are always smooth.

Tydeinae n. subfam.

Prodorsum recurved with two eyes; opisthosoma with three pairs of lyrifissures (*ip* absent); two pairs of genital acetabula, eugenitals only in ♂, progenital aperture longitudinal in ♂; without a cis-acetabulal area in nymphs; epimeral formula (3-1-4-2) in adults, coxal organ present; leg chaetotaxy reduced; at maximum, with five eupathidia on tarsus I, eupathidia absent on other segments; setae *tr* II and IV absent, others may sometimes be absent; two solenidia on the legs (ω I and ω II, latter missing in a few cases); simple anabasis; terminal eupathidium of the palp tarsus seemingly double.

The anagenesis of the Tydeinae is characterized by the appearance of the empodial claw in some genera, the development of paraproctal suckers or the lengthening of chelicera in others. The subfamily is cosmopolitan and occurs in many habitats including soil, plants, birds, and mammals.

Based on the data gathered, other subfamilial classifications for the Tydeidae could be proposed : Meyerellinae and Triophtydeinae could be combined as a single group, as could the Tydeinae and Pretydeinae. On the other hand, the Pronematinae and Tydaeolinae seem quite distinct in all aspects. *Australotydeus* has the typical habitus of a tydeine, but the two groups differ in organotaxy.

2. *Generic level*

Even after having applied the CAMIN and SOKAL approach, the problem of defining the genera of Tydeidae is not solved. Indeed, several classifications may be built on a single genealogical tree. Moreover, this genealogy is far from being finalized and needs further inputs on new species and on the ontogeny of already described species. Certainly the most predictable character states used in cladistic analyses of tydeid subfamilies were derived from leg chaetotaxy. As a consequence, grouping species with too different chaetotaxies seemed a debatable option. Therefore, generic units have been defined by a particular chaetotaxy (defined on all the stases when possible) and on certain related chaetotactic characters (16). As a result, the number of genera has been increased substantially, although some previously recognized genera have been united. Some arguments could be advanced against this extensive division at the generic level.

STRANDTMANN (1967) feels there are too many tydeid genera, but such a statement is without meaning as long as generic criteria are not defined. In fact, the problem is more a matter of the magnitude of the gaps between the genera than a matter of number.

MAYR (1969) states that « splitters » almost without exception classify characters rather than groups of organisms. Inasmuch as a taxon is recognized by a particular combination of characters, and since a set of characters express the individuality of a taxon, this statement is difficult to accept. It is true that some genera in the classification presented here are monospecific, especially in the Triophtydeinae. However, it is not surprising that this primitive group is represented only by a few species representing different genera which probably were much richer in earlier times. A great number of tydeid species probably remain to be discovered, even in the Triophtydeinae, so that there is little chance that any genus will remain monospecific for long.

It is felt that chaetotaxy provides a sound basis for that generic division in the Tydeidae, at least at our present state of knowledge. The gaps between the genera proposed are based on particular chaetotaxies; i.e. they are of the « all of none » type. It should be remembered also that every change in the adult often means changes through ontogeny, i.e. through several stases. This does not mean that a great number of specific variations may not be played on a single chaetotactic theme, or that several adaptive characters may not arise from a single chaetotactic pattern.

The subfamilies and genera of Tydeidae are listed below. The Australotydeinae is a very special subfamily (see diagnosis above), and is monogeneric and monospecific. The Meyerellinae comprises only two genera, *Meyerella* and *Pseudotriophtydeus*, with four species. The shape of the bifurcate idiosomal setae is not considered a subfamilial character. At the present time, the Pretydeinae comprise only six species distributed in two new genera which differ in their solenidiotaxy and anabasis. It would have been pointless to create a subfamily for *Prelorryia*, which differs from the five other species in these characters. Reducing the above criteria to the specific level also would not provide a consistent solution. Therefore, it was necessary to create two genera. The Pronematinae illustrate many new chaetotactic formulae, and others must be expected when new species are discovered. The genus *Proctotydaeus* is returned to the Tydeidae, from which it was removed by BAKER (1965). FAIN and EVANS (1966) pointed out that the genus was closely related to the Tydeidae. The Triophtydeinae comprise new genera. Many of them are represented by species from Antarctica described by STRANDMANN (1967), who was unable to key them out with BAKER's (1965) key. Other problems arose in that any species

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(16) A related chaetotactic character would be one which is not significant at a generic level. For instance, *ft''* I may be eupathidial or not, in almost every group. This is obviously not a generic character.

with three eyes and an undivided femur IV was assigned to the genus « *Triophtydeus* » regardless of the chaetotaxy. The genus « *Triophtydeus* » is not included in this treatment since its chaetotaxy is unknown. The type, which is in the Oudemans collection at Leiden, is in need of remounting before additional study will be possible. Since a synonymy is easier to correct than an homonymy, it is considered advisable not to use « *Triophtydeus* » until the generic type can be studied again. The Tydaeolinae is a quite homogenous subfamily. Only the genera *Pseudotydeus* and *Lasiotydeus* seem somewhat atypical. Both are discussed in the fourth part. Some new tydaeoline genera are described because of the diversity of their leg chaetotaxy. The Tydeinae represent the biggest tydeid subfamily. Unfortunately, their systematic history is extremely confused. A single genus was found to include several species with different — sometimes very different — chaetotaxies, while species with identical chaetotaxy were distributed in several genera. This confusion arose because of adherence of many recent workers to the old generic concept of Canestrini, Berlese, Thor and Oudemans, a concept which was based mainly, or only, on variations in skin ornementation. The systematics of the Tydeidae has been completely reorganized in this interpretation.

Australotydeinae : *Australotydeus* Spain 1969.

Meyerellinae : *Meyerella* Baker 1968; *Pseudotriophtydeus* n. gen.

Pretydeinae : *Pretydeus* n. gen.; *Prelorryia* n. gen.

Pronematinae : *Apopronematus* n. gen.; *Homeopronematus* n. gen.; *Metapronematus* n. gen.; *Naudea* Meyer & Rodrigues 1965; *Parapronematus* Baker 1965; *Pausia* Kuznetzov & Livshitz 1972; *Proctotydaeus* Berlese 1911 sensu Fain & Evans 1966; *Pronecupulatus* Baker 1965; *Pronematulus* Baker 1965; *Pronematus* Canestrini 1886 sensu Baker 1965.

Triophtydeinae : *Apotriophtydeus* n. gen.; *Metatriophtydeus* n. gen.; *Pretriophtydeus* n. gen.; *Teletriophtydeus* n. gen; (+ one generic unit : TR1) (17).

Tydaeolinae : *Aesthetydeus* n. gen.; *Coccotydaeolus* Baker 1965; *Lasiotydeus* Berlese 1908, *sensu* Baker 1965; *Metatydaeolus* n. gen.; *Microtydeus* Thor 1931, *sensu* Baker 1965; *Paratriophtydeus* Baker 1965; *Paratydaeolus* n. gen.; *Primotydeus* n. gen.; *Pseudotydeus* Baker & Delfinado 1974; *Tydaeolus* Berlese 1910, *sensu* Baker 1965; *Tyndareus* Livshitz & Kuznetzov 1972; (+ one generic unit, G1) (17).

Tydeinae : *Afrotydeus* Baker 1970; *Apolorryia* n. gen.; *Eotydeus* Kuznetzov 1973; *Homeotydeus* n. gen.; *Idiolorryia* n. gen.; *Krantzlorryia* n. gen.; *Metalorryia* n. gen.; *Neolorryia* n. gen.; *Orthotydeus* n. gen.; *Perafrotydeus* n. gen.; *Tydeus* Koch 1835, n. comb.; *Tydides* Kuznetzov 1975; (+ two generic units, TY1 and TY2) (17).

Generic descriptions and keys are presented in part IV.

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(17) To describe a new genus from one or two specimens is felt to be inadvisable except when the specimen(s) exhibit very special characteristics. However, it may be useful to indicate the existence of its chaetotactic pattern. Therefore, some generic units are acknowledged but are not officially described.

3. *Infrageneric or specific level*

Some new genera are monospecific but, as noted earlier, for most of them, this is not likely to be a permanent situation. A great number of new tydeid species is expected to be described. The old systematics was an obstacle to such an achievement because of its lack of consistency.

At the present time, for each taxon described by a particular chaetotactic formula, a great deal of variation may be expected in the condition of chelicerae, empodia, setae, and striations, and in the clustering of certain setae... For example, in the collection kindly sent by Dr. Marshall, several species were labelled as « *Coccotydaeolus* sp. » based on the old classification. These species were extracted from different types of litter and are distinctive in their pattern and density of striation, setal shape, and sensilla. All of these characters will have to be considered in the future for proper species identification.

Dr. Marshall's collection also is interesting from an ecological point of view in that it reveals that the Tydeidae may be expected to occur in a particular habitat type, as already suggested by André (1975, 1979). But, once again, serious ecological studies require precise specific identification, or at least, they must rest on strong generic concepts. Misidentifications of tydeids have had some interesting zoogeographical consequences. For instance, *Tydaeolus frequens* is thought to occur in many locations throughout the world. However, the drawings of the sensillum published by Weis-Fogh (1948) and Wood (1965) suggest that there are, in fact, several species. It is significant that the minute size of seta l'' on tibia I of *Tydaeolus frequens* as described by Grandjean (1938*b*) has never since been recorded in other collections of this « species ».

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APPENDIX I : GLOSSARY OF SPECIAL TERMS

Amphistasy : the quality of state of being amphistatic (ant. eustasy).

Amphistatic : not appearing at a particular stase (ant. eustatic).

Anabasis : migration of either or both proral setae of tarsus to the position of the tectal setae (see part III).

Anhomologous Tautergy : repetition through ontogeny of a particular morphological character of (a) well defined organ(s) when the organs bearing this character are not the same from one stase to another but apparently keep the same location on the animal (adapted from Grandjean, 1964 : 170).

Anomaly : individual and exceptional variation of any nature, almost always unilateral, to which no evolutionary significance may be attributed in the present state of knowledge (Grandjean, 1972 : 455).

Atrichosy : state or quality of an area or of a segment that has lost all of its setae.

Bisynthesis : disappearance of an idiosomal seta followed by the movement of the remaining element of the pair onto the sagittal plane (see part II).

Chaetotaxy : see organotaxy.

Designation : a nomenclature system not based on idionymy but generally resting on location (cf. notation).

Disjunction : distal migration of either member of a setal pair on a leg segment.

Error : variation of all or none (see anomaly, vertition).

Eustasy : the quality or state of being eustatic (ant. amphistasy).

Eustatic : appearing at a particular stase (ant. amphistatic).

Idionymic : relating to a particular organ as distinct from other organs of the same nature. Consequently, an idionymic organ may be named; for example, a pair of setae is called « prorals » since they may be distinguished from all other tarsal setae, even when they migrate.

Idionymy : the quality or state of being idionymic.

Neotrichy : state or quality of being neotrichial (ant. prototrichy).

Neotrichial : referring to an area, a segment or an animal some setae of which are secondarily formed (ant. prototrichial).

Notation : a nomenclative system based on idionymy (cf. designation).

Organotaxy : Distribution pattern or « taxy » of organs — specifically their number and their location. Organotaxy comprises chaetotaxy (setae), phanerotaxy (setiform organs), solenidiotaxy (solenidia), poroidotaxy (lyrifissures), sigillotaxy (muscle insertions), and adenotaxy (glands).

Orthotrichy : state or quality of being orthotrichial.

Orthotrichial : referring to an area, a segment or an animal the setae of which keep their primitive and original location.

Paleotrichy : state or quality of being paleotrichial.

Paleotrichial : referring to a prototrichial area, segment or animal which keeps all the primitive setae.

Parallel Homology : an hypothesis referring to a primitive state where each leg segment is supposed to be identical on all four legs.

Phanerotaxy : see organotaxy.

Poroidotaxy : see organotaxy.

Priority list : a method for ranking setae according to their frequences of occurrence, in the normal or eupathidial state, from the strongest (high frequencies) to the weakest (low frequencies). Grandjean (1942) distinguished four types of priority lists ontogenetic, vertitionel, metameric, and phylogenetic.

Prototrichy : state or quality of being prototrichial (ant. nectrichy).

Prototrichial : referring to an area, a segment or an animal the setae of which are primitive (ant. neotrichial).

Sigillotaxy : see organotaxy.

Solenidiotaxy : see organotaxy.

VERTITION : a fundamentally unilateral « all or none » variation in an idionymic organ which is observed in individuals of the same species and at the same stase, which may be considered to have an evolutionary significance (from GRANDJEAN, 1972 : 455).

APPENDIX II :

LIST OF ABBREVIATIONS AND SYMBOLS

acm : anteroculminal seta (palptarsus);
ad1, ad2 : adoral seta;
ag1 to *ag5* : aggenital setae;
ba : basal seta (palptarsus);
cot : cotyloid cavities;
cpc : podocephalic canal;
d : dorsal seta (on a leg segment);
d1 to *d5* : first five setae of the paraxial alignment of the dorsal face of opisthosoma;
das : disjugal — abjugal — sejugal furrow;
dg : dorsogenual seta (palpgenu);
dg3 : third ductus of podocephalic canal;
eI and *ep* : supracoxal spines (on leg I and palp);
em : empodium;
eu1 to *eu6* : eugenital setae;
ft : fastigial seta (tarsus);
ge1 to *ge6* : genital setae;
h1, h2 : setae of segment H;
H : segment anterior to the pseudanal segment (PS);
ia, im, ip and *ih* : lyrifissures;
it : iteral seta (tarsus);
k″ : famulus;
k.ph : condylophore;
l : lateral seta (on a leg segment);
l1 to *l5* : first five setae of the antiaxial alignment of the dorsal face of opisthosoma.
ma, mb1, mb2, mc, md, mds, me, mes : dorsal sigilla on opisthosoma;

n.st. : neostigma;
N1, N2, N3 : the three nymphs;
ol : lateral claw;
om : empodial claw;
p : proral seta (tarsus);
p1 to *p3* : prodorsal setae;
ps : pseudanal seta;
pv : proximoventral seta (femur);
s : sensillum;
sc1 and *sc2* : subcapitular setae;
smd : furrow posterior to *das*;
sti and *stπ* : stigmata (anti- and paraxial);
t : seta on palptibia;
tc : tectal seta (tarsus);
tr : trochanteral seta;
tr α, *tr* π : anti- and paraxial tracheae;
u : unguinal seta (tarsus);
v : ventral seta (on appendages);
vs : vestibulum;

α : antiaxial;
δ : dehiscence line;
ζ : eupathidial;
π : paraxial;
φ : tibial solenidion;
ω : tarsal solenidion;

1*a*, 1*b*, 1*c*, 2*a*, 3*a*, 3*b*, 3*c*, 3*d*, 4*a*, 4*b*, 4*c* : epimeral setae.

CONSEIL D'ADMINISTRATION POUR L'ANNÉE 1979

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Dhr. A. Coomans,
M. Ch. Jeuniaux,
Dhr. Ph. Polk.
Dhr. H. Koch,
M. A. Quintart,
M. W. Van den Bruel.

PROCÈS-VERBAUX DES SÉANCES DE LA SOCIÉTÉ EN 1978

VERSLAGEN VAN DE ZITTINGEN VAN DE VERENIGING IN 1978

Assemblée Générale ordinaire du 21 janvier 1978
Algemene Vergadering van 21 januari 1978

L'Assemblée se tient à la Fondation Universitaire sous la présidence de M. W. Verheyen, Président.

De vergadering heeft plaats in de Universitaire Stichting onder het voorzitterschap van de Heer W. Verheyen, Voorzitter.

1. *Approbation du Procès-verbal de l'Assemblée générale du 22 janvier 1977. — Goedkeuring van het verslag van de Algemene Vergadering van 22 januari 1977.*

2. *Rapport de M. J.-J. Van Mol sur la publication des Annales. — Verslag van de Heer J.-J. Mol over de publikatie van de Annalen.*

M. J.-J. Van Mol indique les avantages qu'a apporté le changement de typographie des Annales. Cela représente une économie substantielle en argent et en papier. Les 245 pages du tome 106 correspondent à 420 pages de l'ancienne typographie. M. Van Mol espère maintenir le rythme des publications. Il fait appel aux auteurs pour que ceux-ci lui confient immédiatement des manuscrits. L'Assemblée demande que le retard soit rattrapé le plus vite possible. M. Verheyen félicite M. Van Mol pour son action particulièrement profitable pour la Société et les forêts.

3. *Rapport de Madame H. Herlant-Meewis, Bibliothécaire. — Verslag van Mevr. H. Herlant-Meewis, Bibliothecaresse.*

M^{elle} J. Naisse présente le rapport de M^{me} H. Herlant-Meewis, excusée. 240 exemplaires des deux fascicules du tome 106 sont en cours d'expédition à l'étranger : ceux-ci ont été envoyés aux membres par le Secrétaire-général.

La Bibliothèque est tenue à jour grâce à M^{me} Baert. A la suggestion de M. Deligne, l'Assemblée accepte l'échange de nos Annales avec les « Publications of the Centre for Overseas Pest Research » de Londres. L'échange avec la revue Mediterranea est provisoirement refusé. Le Président remercie toute l'équipe qui gère la Bibliothèque, c'est-à-dire le bien le plus précieux de la Société.

4. *Rapport de M. J. Van Goethem, trésorier. — Verslag van de Heer J. Van Goethem, penningmeester.*

De Heer J. Van Goethem legt de balans der ontvangsten en uitgaven met betrekking tot het jaar 1977 voor, alsook het ontwerp van budget voor het jaar 1978. Hij benadrukt dat het financieel mogelijk is een deel van de achterstand in de publikatie der Annalen in te lopen. Op voorstel van de Heren O. Van der Borght en W. De Smet, die door de vergadering als verificateurs werden aangeduid, worden de rekeningen voor het dienstjaar 1977 goedgekeurd.

Nadien wordt gediscussieerd over de drukkosten der Annalen en over de vertraging van één jaar in het verschijnen van ons tijdschrift. De Heer J.-J. Van Mol herinnert eraan dat door het nieuwe lettertype het aantal pagina's dat per artikel gratis gedrukt wordt, van 16 op 12 wordt teruggebracht. Het aantal gratis platen blijft twee.

In verband met de aangevraagde subsidies, schetst de Heer Ch. Jeuniaux de moeilijke toestand van de Universitaire Stichting. De Heer J. Van Goethem besluit dat het ideaal zou zijn indien in elke jaargang één omvangrijk artikel of een artikelenreeks zou gepubliceerd worden met ruime financiële tussenkomst van de auteur(s). De Voorzitter dankt de Heer Van Goethem voor de grote toewijding waarmee hij zijn functie uitvoert.

5. *Conclusions du Président. — Besluiten van de Voorzitter.*

De Heer W. Verheyen brengt hulde aan de Heer G. Vandebroek, oud-voorzitter van onze Vereniging, die in het voorbije jaar overleden is. De Vergadering houdt, rechtstaande, een minuut stilte in acht ter nagedachtenis van de overledene.

De Voorzitter brengt ter kennis van de leden dat Mevr. H. Herlant-Meewis tot erelid benoemd werd van de « Société zoologique de France ».

Vervolgens somt de Voorzitter de activiteiten op van de Vereniging. Hij dankt de onderzoekscentra waar de Vereniging te gast was en hij feliciteert de Heer Ph. Lebrun voor de activiteiten van de afdeling oecologie en ethologie der dieren. De Voorzitter vermeldt de bijzondere inspanningen die de Beheerraad en de Commissie voor herziening der statuten tijdens het afgelopen jaar hebben verricht. Hij leest het verslag voor van R.P. A. Bauchau over het functionneren van de Vereniging. Hij dankt de Secretaris-generaal die de activiteiten organiseert en aan elk lid de uitnodigingen en de afleveringen der Annalen toestuurt, zelfs indien dit lid driemaal in een jaar verhuisd is.

Tot besluit keurt de Algemene Vergadering het beleid van zijn beheerders goed.

6. *Élections statutaires. — Statutaire verkiezingen.*

Sur proposition du Conseil d'Administration, sont élus ou réélus à l'unanimité :

M^me^ H. Herlant-Meewis, bibliothécaire.

M. J. Van Goethem, trésorier.

M. A. Quintart, secrétaire général qui n'accepte ce renouvellement de mandat que pour un an.

MM. Bauchau, Jeuniaux, Koch et Polk sont réélus membres du bureau.

7. *Le calendrier des réunions est mis au point. — De kalender der vergaderingen wordt vastgesteld.*

8. *Présentation de nouveaux membres. — Voorstelling van nieuwe leden.*

Dhr. Ch. de Vroey, Doctor in de wetenschappen, voorgesteld door W. Verheyen en J. Van Goethem.

Dhr. H. M. Van den Bergh, documentalist in dierkunde, voorgesteld door H. Koch en A. Quintart.

M. E. Feytmans, Dr. en Sciences, groupe zoologie, présenté par R.P. Bauchau et M. Micha.

Le Président lève la séance et ouvre immédiatement l'Assemblée générale extraordinaire.

Assemblée générale extraordinaire du 21 janvier 1978
Buitengewone algemene vergadering van 21 januari 1978

Cette deuxième assemblée générale extraordinaire a pour objet la proposition de modification des statuts. Le nombre des membres présents s'élèvent à 27, 2 procurations ont été déposées.

M. Verheyen, président, expose les grandes lignes du projet de modification. Il donne lecture de la lettre de M. Max Poll qui demande de ne pas changer les statuts. MM. De Coninck et Jeuniaux interviennent et soutiennent la modification des statuts. M. Van den Bruel demande que le titre des Annales soit modifié le moins possible.

L'Assemblée vote les modifications article par article, puis chapitre par chapitre enfin sur l'ensemble des statuts modifiés.

Art. 1 : 28 voix pour, 1 contre; adopté.
Art. 2 : 20 voix pour, 9 contre; adopté.
Art. 3 : unanimité des membres présents; adopté.
Art. 4-73 : unanimité des membres présents; adopté.
Ensemble des statuts : 27 voix pour, une abstention, une voix contre.

Les statuts modifiés sont adoptés. Ils ont été publiés au *Moniteur belge* dans les annexes du 24 août 1978; p. 3273, n° 7125.

M. W. Verheyen, président, remercie les membres présents et les membres de la Commission des statuts qui ont sacrifié leur temps pour assurer l'avenir de la Société. Il lève la séance.

Réunion commune du 20 mai 1978
Gemeenschappelijke Vergadering van 20 mei 1978

« L'apport de l'écologie dans l'évolution biologique des paysages et l'aménagement des territoires ».

Section écologie et systématique de la Société royale de Botanique
Afdeling Ecologie en Systematiek van de Koninklijke Vereniging voor Plantkunde
et Section écologie et éthologie animale.
en Afdeling Ecologie en Ethologie der dieren.

La réunion se tient à Louvain-la-Neuve sous la présidence de M. Ph. Lebrun, coordinateur de la section écologie et éthologie animales. M. P. Berthet, Doyen de la Faculté des Sciences, accueille les participants.

Communications de nos membres :

L. Nef : « *Considération sur l'évaluation biologique de l'espace non-urbain* ».

Résumé de l'auteur :

La valeur biologique de l'espace non-urbain doit être estimée par sa « qualité biologique intrinsèque ». Celle-ci peut se définir en partant des grandes bois régissant l'évolution des « organismes » à tous les niveaux d'organisation (individu, communauté, et même groupe humain) : la Vie tend vers des systèmes à y ont des complexité, diversité, rareté de plus en plus élevées; la qualité biologique est donc exprimable par ces caractéristiques. On peut en déduire aussi des arguments pour le choix de critères qui, pour être valables, doivent s'avérer en corrélation avec ladite qualité biologique. Les autres critères (de production, ou de conservation, tels l'étendue, l'isolement) ont une destination et ne peuvent informer valablement sur la qualité biologique d'un territoire. Parmi les critères acceptables, citons surtout la diversité, la rareté (au sens biologique réel : spécialisation), la complexité; ces critères sont, surtout pour des raisons de facilité, le plus souvent appliqués aux végétaux supérieurs et aux oiseaux. Quelques exemples d'application sont donnés et commentés.

Discussion : J. Duvigneaud; H. Stieperaere; M. Dumont.

R. Tercafs : « *Apport de l'informatique à l'évaluation biologique des sites* ».

Cette communication est publiée dans ce fascicule.

Discussion : P. Berthet; P. Pierard; Ph. Lebrun; J. Duvigneaud.

J. Leclercq : « *La cartographie sur quadrillage, outil pour estimer objectivement diversité, chance et risque dans les faunes locales* ».

Résumé :

En 1969, les zoologistes européens, taxonomistes et faunisticiens s'occupant d'Invertébrés, ont été invités à participer à un projet coopératif et de longue haleine que nous avons appelé « *The European Invertebrate Survey — Cartographie des Invertébrés Européens — Erfassung der Europäischen Wirbellosen* ». L'objectif final de ce projet est le même que celui d'autres organisations biogéographiques européennes et notamment que celui du « Committee for Mapping the Flora of Europe » puisqu'il s'agit d'établir des cartes de répartition d'espèces à l'échelle du continent, avec un minimum de normalisation, celle-ci étant assurée d'abord par l'adoption du quadrillage U.T.M. avec subdivisions décimales.

Pour la plupart des groupes d'Invertébrés, cet objectif final est lointain, très lointain, voire même utopique. Mais notre organisation s'est montrée réaliste et patiente en préconisant, pour commencer, des opérations cartographiques nationales et régionales, l'édification de fichiers aussi normalisés de données fauniques, l'exploitation de ces informations pour répondre à des questions en rapport avec les problèmes particuliers de la conservation de la nature, de l'aménagement et de la gestion des territoires.

Dans cette vaste entreprise, l'apport des zoologistes belges a été pionnier, efficace, tenu pour un modèle. Notre équipe de Gembloux s'est beaucoup dépensée pour qu'il en soit ainsi, mais on nous a aussi bien compris et beaucoup aidé, en Flandre comme en Wallonie, du côté des chercheurs professionnels et du côté des amateurs, pour les Insectes et pour d'autres classes d'Invertébrés. L'expression la plus spectaculaire de nos activités, c'est la publication, de 1970 à ce jour, de 1458 cartes toujours qualifiées de provisoires.

En outre des fichiers normalisés selon les recommandations de notre projet international fournissent d'autres éléments pour apprécier l'abondance et les chances des espèces. On y trouve notamment le nombre d'individus notés (observés ou récoltés), le nombre de dates où l'espèce à été observée (ou capturée), le nombre d'années, la dernière année ou l'espèce a été vue. Autant de critères qu'il est opportun de confronter.

Hélas, les premières analyses que nous avons faites avec ces critères nous ont fait retenir l'hypothèse que l'entomofaune de la Belgique se détériore gravement. Nous estimons à 10 % environ et c'est peut-être davantage, le nombre d'espèces en nette régression en Belgique depuis 1950!

Discussion : J. Duvigneaud; L. Nef.

M. T. Fontaine : « *Apport de la cartographie dans l'estimation du degré d'altération des cours d'eau* ».

Cette communication est publiée dans ce fascicule.

Discussion : J. Leclercq; Ph. Lebrun; Ch. Jeuniaux; P. Pierard; G. Josens.

Vergadering van zaterdag 18 november 1978

Réunion du samedi 18 novembre 1978

De vergadering heeft plaats in de lokalen van de Universitaire Instelling Antwerpen, georganizeerd door het departement biologie.

1. *Voorstelling van nieuwe leden. — Présentation de nouveaux membres.*

Dhr. F. Bernaerts, Mej. G. Gabriels : licentiaten in de Dierkunde en Mw. Ch. Van den Branden, doctor in de Dierkunde, voorgesteld door W. Verheyen en W. Decleir.

Dhr. R. Verhagen en Dhr. L. Vermeiren, licentiaten in de Dierkunde, voorgesteld door W. Verheyen en J. Hulselmans.

Mej. E. Lodewijckx en Dhr. J. Van Rompaey, licentiaten in de Dierkunde, voorgesteld door W. Verheyen en F. De Vree.

Dhr. D. Meirte, licentiaat in de Dierkunde, voorgesteld door D. Thys van den Audenaerde en F. De Vree.

2. *Mededelingen. — Communications :*

V. Coeckelberghs : « *De mogelijkheid om de kleurpatronen van cichliden te gebruiken als indicatoren voor de veroorzaking van gedrag* ».

Samenvatting van de auteur :

Aan de hand van een kwantitatieve analyse van het gedrag van de Tanganyika cichlide *Limnotilapia dardennei* werd aangetoond dat de kleurpatronen van dit dier kunnen worden beschouwd als de uitdrukking van de stemming, de motivatietoestand waarin het dier op dat ogenblik verkeert.

Een multivariabele analyse, de correspondentie analyse, resulteerde inderdaad in een model van de patroongebondenheid van het gedrag : het waargenomen gedrag werd ingedeeld in groepen die gekarakteriseerd worden door een gelijkaardig patroongebonden optreden. Werd deze groepering van gedragingen vergeleken met de causale organisatie van het gedrag, nl. een indeling in groepen van gedragingen die toe te schrijven zijn aan gemeenschappelijke veroorzakende factoren, dan bleken beide indelingen volledig met elkaar in overeenstemming. Bijgevolg kon worden besloten dat elk kleurpatroon kan worden beschouwd als een indicator voor het veroorzakend mechanisme dat aan het geobserveerde gedrag ten grondslag ligt.

Dit zal in het vervolg toelaten de kleurpatronen van de cichlide *Limnotilapia dardennei* in te schakelen in de kwantitatieve analyse van gedragsproblemen, als parameters voor de veroorzaking van gedrag. Deze toepassing zal vooral daar belangrijk zijn, waar openlijk gedrag achterwege blijft of waar gedrag de resultante is van twee gelijktijdig of alternerend geactiveerde motivatietoestanden.

Discussie : W. Verraes.

L. Hanon : « *Contribution à l'étude de l'incubation buccale chez les poissons cichlidés. Gevolgd door een 16 mm film. — Projection d'un film 16 mm* ».

Discussion : Thys van den Audenaerde; A. Coomans; W. Verraes.

M. Nelissen : « *Het belang van het functioneel ethologisch onderzoek voor de evolutiestudie van het gedrag* ».

Deze mededeling zal gepubliceerd worden in aflevering 109 van de Annalen.

Discussie : W. Verraes; W. Decleir; A. Coomans.

W. VERRAES : « *De ontwikkeling der pharyngeale kaken en de neurocraniale apophyse bij* Haplochromis elegans (*Teleostei : Cichlidae*) ».

Samenvatting van de auteur :

Op grond van series microscopische doorsneden doorheen de kop van buccale en postbuccale ontwikkelingsstadia van *Haplochromis elegans* werd de ontwikkeling van de neurocraniale apophyse in de schedelbasis histologisch en via grafische rekonstrukties bestudeerd. Dit onderzoek vormt een onderdeel van het ontogenetisch onderzoek van heel de kopstreek (harde en weke delen). In de loop der ontogenie zien we dat achtereenvolgens eerst het os parasphenoideum alleen, later ook het os basiocriptale (en misschien zelfs de tip van het os prooticum) het lichaam van de apophyse gaan opbouwen. Deze bevindingen passen in het kader van de hypotese geformuleerd door vergelijking van adulte Cichliden, waarbij het *Tylochromis*-type van apophyse als het meest eenvoudige wordt beschouwd en het *Haplochromis*-type als een ingewikkelder.

Voor wat de ontogenie der pharyngeale kaken zelf betreft, kan gezegd worden dat de bovenste pharyngeale kaken worden opgebouwd door (I) het infrapharyngobranchiale II, (2) het infrapharyngobranchiale III + IV, en (3) een dermale tandplaat zonder kraakbenige voorfaze.

De verbeningen van infrapharyngobranchiale II en vooral van infrapharyngobranchiale III + IV zijn zeer interessant : naast perichondiale verbening, kraakbeen afbraak en vervanging door been (endochondrale beenvorming) en de aanleg van dermale tandplaten (waarop semi-mobiele tanden vastzitten), werden ook aanduidingen van rechtstreekse verbening van het kraakbeen gevonden. Om meer zekerheid over dit laatste te krijgen, zal in de nabije toekomst ook histochemisch onderzoek plaats grijpen.

Discussie : Thys van den Audenaerde; M. Chardon; W. Verheyen.

F. GHIOT : « *Différents moyens de mouvoir les barbillons chez les Bagroidei* ».

Discussion : M. Chardon.

D. MEIRTE : « *De kauwbewegingen bij* Tachyoryctes ruandae (*Rodentia*) ».

Samenvatting van de auteur :

Aan de hand van de schedel werden de vrijheidsgraden van het systeem bepaald. Filmanalyse-resultaten werden met een spline-interpollatie methode uitgemiddeld, zodat verschillende voedseltypes konden vergeleken worden. De beweging werd vervolgens in termen van de besproken vrijheidsgraden beschreven, hiertoe werd een model van de fossa ingebouwd. De onderlinge positie van de aktieve molarenbattereijen kon worden gevolgd via een ruimtelijk model van de molaren. Dit laatste is nog niet volledig bewijskrachtig maar suggereert reeds de grote invloed van de positie van de voedselbolus in de effectieve beweging tijdens de kauw-fase. Verder onderzoek wordt verricht.

Discussie : J. Hulselmans.

L. PATUREAU et M. CHARDON : « *Nage et structure de la colonne vertébrale chez* Ictalurus nebulosus ».

Discussion : W. De Smet, W. Verraes.

F. DE VREE et B. DE MEY : « *Het kauwpatroon van vliegende honden* Pteropus giganteus ».

Discussie : J. Hulselmans; W. Verraes.

Réunion du 16 décembre 1978

Vergadering van 16 december 1978

La réunion se tient à l'Institut royal des Sciences naturelles de Belgique sous la présidence de M. W. Verheyen, président. — De vergadering heeft plaats in het Koninklijk Belgisch Instituut voor Natuurwetenschappen te Brussel onder het voorzitterschap van de Heer W. Verheyen, voorzitter.

1. *Présentation de nouveaux membres. — Voorstelling van nieuwe leden.*

Dhr. R. MARQUET, licentiaat in de Dierkunde, voorgesteld door W. Verheyen en J. Van Goethem.

Dhr. B. GODDEERIS, W. ROGGEMAN en J. PAULUSSEN, licentiaten in de Dierkunde, voorgesteld door J. Van Goethem en K. Wouters.

Dhr. L. BAERT en F. DE MEUTER, doctors in de Dierkunde, voorgesteld door J. Van Goethem en K. Wouters.

2. *Communications. — Mededelingen :*

C. VAN DEN BRANDEN en W. DECLEIR : « *Studie van de accessoire nidamentaalklier van* Sepia officinalis *L.* ».

Deze mededeling werd gepubliceerd in dit nummer. Cette communication est publiée dans ce fascicule.

Discussie — Discussion : J.-J. Van Mol.

H. REYNERS, E. G. DE REYNERS et J. R. MAISIN : « *Altérations du cortex cérébral du rat causées par certains facteurs de l'environnement* ».

Résumé des auteurs. — Samenvatting van de auteurs :

Malgré l'importance de ses défenses externes et internes (dont la barrière hématoencéphalique), le cerveau est sensible à divers facteurs de l'environnement. On a cherché à déceler par morphométrie les constituants cellulaires les plus vulnérables. Il ressort de ces études que certains types gliaux (les oligodendrocytes) constituent de véritables cellules cibles pour les radiations ionisantes (RX) ainsi que pour les métaux lourds (Pb). Ce type cellulaire s'avère, en fait, être le bioindicateur morphologique cérébral le plus sensible connu actuellement; la densité de ces cellules est significativement (et définitivement) abbaissée par une irradiation de 2200 R sur le cerveau à l'âge de 3 mois. Ce phénomène est déjà décelable avec une dose de 550 R, au 15^e jour après l'irradiation. D'autre part, la présence de plomb (dès le seuil de 0,01 %) dans l'alimentation détermine aussi une diminution des oligodendrocytes, mais elle est ici « compensée » par une augmentation des astrocytes et de la micrologie, les 2 autres types cellulaires gliaux. Ce phénomène est beaucoup plus net aux doses fortes (jusqu'à 1 %). Les relations de satellitisme des cellules gliales vis-à-vis des neurones sont elles aussi modifiées.

Discussion — Discussie : Ph. Lebrun; G. de Ridder-Valentin; H. Koch; A. Bauchau; W. Verheyen.

Mej. A. DHONDT : « *De Pteriomorphia* (*Bivalvia*) *uit het type Maastrichtiaan* ».

Deze mededeling werd gepubliceerd in dit nummer. Cette publication est publiée dans ce fascicule.

Discussie — Discussion : W. Verheyen.

Z. DARTEVELLE, M. MARLIER et G. MARLIER : « *Mise en évidence de l'anatomie externe des Arthropodes par digestion bactérienne des organes internes* ».

Cette communication est publiée dans ce fascicule. Deze mededeling werd gepubliceerd in dit nummer.

Discussion — Discussie : Ch. Jeuniaux; H. Reyners; Ph. Lebrun.

RECHERCHE DANS LE DOMAINE DE L'ENVIRONNEMENT

Récemment est parue la publication *Recherche dans le domaine de l'environnement en Belgique*. Cet inventaire donne un large aperçu des travaux de recherches qui ont été réalisés dans ce domaine au cours des dernières années dans notre pays. Les 760 projets de recherche cités sont décrits en détail.

Le volume 1 (Projets) contient pour chaque institution : le nom, l'adresse et l'appareillage/installations spécifiques. Les données suivantes sont fournies pour chaque projet : les noms des chercheurs, la durée de la recherche, les méthodes utilisées, les possibilités d'application et les bénéficiaires (ceux au profit de qui la recherche a été faite).

Le volume 2 (Index) contient en plus d'une table des matières une liste de chercheurs et trois listes de mots-clés (néerlandais, français, anglais) destinées à faciliter la recherche.

Cette publication en deux volumes peut être obtenue au C.N.D.S.T. au prix de 300 FB (Bd. de l'Empereur 4, B-1000 Bruxelles).

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La publication des articles dans les *Annales* est soumise aux conditions suivantes :

1. L'auteur doit être membre de la Société, en règle de cotisation.
2. Le manuscrit doit être approuvé par le Comité de Rédaction de la revue.
3. Les articles ayant fait l'objet d'une communication verbale à une des séances de la Société seront publiés prioritairement.
4. La participation de la Société aux frais de publication se limitera à un cahier de 12 pages pouvant comprendre 4 figures ou 2 planches. Tout dépassement du texte ou des illustrations sera facturé au prix coûtant (voir N.B.).
5. En outre, le manuscrit devra comporter :
   a) une traduction du titre en anglais afin que nos publications puissent être reprises dans les « Biological Abstracts » et les « Current Contents ».
   b) un résumé dans la langue de l'article et un résumé rédigé en anglais.
6. a) Le texte devra être présenté dactylographié dans sa forme définitive. Les mots à composer *en italique* y seront soulignés d'un trait, ceux à composer en PETITES CAPITALES, de deux traits.
   b) Les références bibliographiques dans le texte se feront par l'indication de l'auteur, de l'année et d'un indice éventuel, si plusieurs articles du même auteur sont mentionnés pour la même année. Dans l'index bibliographique, les références se feront comme suit :
   1° pour les périodiques :
   Auteur — Année — Titre de l'article — *Titre abrégé de la revue (en italiques)* — Indication du volume (en chiffres arabes) — Indication de la première page de l'article.
   2° pour les livres :
   Auteur — Année — *Titre (en italiques)* — Éditeur — Lieu d'édition — Nombre de pages.

N. B. Une estimation des frais supplémentaires éventuels peut être obtenue chez le Secrétaire de Rédaction Jean-Jacques VAN MOL c/o Université libre de Bruxelles — Tél. : (02)6490030 (extension : 2230).

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De publikatie van artikelen in de *Annalen* is aan de volgende voorwaarden onderworpen :

1. De auteur dient lid te zijn van de Vereniging en zijn lidgeld betaald te hebben.
2. Het manuscript moet worden goedgekeurd door het redactiecomité van het tijdschrift.
3. De artikelen die het voorwerp uitmaakten van een mededeling tijdens een vergadering van de Vereniging, genieten voorrang bij publikatie.
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   De auteur heeft recht op 50 gratis overdrukken.
   Hij dient schriftelijk zijn goedkeuring met voormelde voorwaarden te bevestigen en eventueel aan te geven op welke naam de factuur dient opgemaakt te worden.

5. Het manuscript moet bovendien bevatten :
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   b) een samenvatting in de taal van het artikel alsook een samenvatting in het Engels.
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   2° Voor de boeken :

   Auteur — Jaar — *Titel* (*in italiek*) — Uitgever — Plaats van uitgave.

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