Ultrastructural analysis of the intestinal contents of *Clarkus papillatus* (Nemata : Mononchina) : ecological interest of the survey

Étienne SAUR and Pierre ARPIN

Muséum national d'Histoire naturelle, Laboratoire d'Écologie Générale, 4, Avenue du Petit-Château, 91800 Brunoy, France.

SUMMARY

The intestinal contents of the ubiquitous nematode species *Clarkus papillatus* (Bastian, 1865) Jairajpuri, 1970 was studied by means of transmission electron microscopy at three levels of the digestive tract (anterior intestine, mid intestinal region and posterior intestine). Three humus types (acid mull, moder and dysmoder) were examined in two periods of the year (autumn and spring). Different cellular aspects linked to alimentation were considered : change of the intestinal contents during digestion, origin and role of electron dense granules observed in the anterior intestine and lamellar or vesicular expansions in the posterior intestine. A variety of food items was confirmed in the intestine of *Clarkus papillatus* : different animal prey, bacteria and clay particles. The double origin of microflora inside the digestive tract (microflora from soil bacterial colonies and microflora from bacterial multiplication inside the intestine, was proved. Its role was considered : microflora was used for food but bacteria had also a lytic action on the digestive content. The ecological interest of this study is discussed.

RÉSUMÉ

Analyse ultrastructurale du contenu intestinal de Clarkus papillatus *(Nemata : Mononchina) : intérêt écologique des observations*

Le contenu intestinal de *Clarkus papillatus* (Bastian, 1865) Jairajpuri, 1970, espèce ubiquiste, a été étudié à l'aide de la microscopie électronique à transmission à trois niveaux de l'intestin (antérieur, moyen et postérieur). Trois types d'humus (mull acide, moder et dysmoder) ont été prospectés sur deux périodes de l'année (automne et printemps). Différents aspects cellulaires liés à l'alimentation ont été abordés : évolution du contenu intestinal au cours de la digestion, origine et rôle des granules opaques aux électrons observés dans l'intestin antérieur et des expansions membranaires ou vésiculaires dans l'intestin postérieur. Est confirmée la présence d'éléments variés de nourriture dans l'intestin de *Clarkus papillatus* : proies animales diverses, bactéries, feuillets d'argile. Est démontrée la double origine de la microflore dans l'intestin : microflore provenant des bactéries du sol et microflore issue d'une multiplication bactérienne active dans l'intestin. Le rôle de la microflore est également considéré : elle intervient dans l'alimentation comme nourriture mais aussi dans la digestion car elle a une action lytique sur le contenu digestif. L'intérêt écologique de ces observations est discuté.

For a long time nematologists have been interested in predatory nematodes of the Mononchina, seeing in them a possibility for biological control of phytoparasitic nematodes (Cobb, 1913; Steiner & Heinly, 1922; Cohn & Mordechai, 1974; Small, 1979; Azmi, 1983). Recent research provides more detailed information about the predatory behaviour of these animals, their diets and the factors which influence predation. The most important studies can be found in the excellent compilation by Small (1987).

Arpin and Kilbertus (1981) particularly used transmission electron microscopy in order to define the constituent elements of the alimentary bolus and ways of digestion of these substances. In contrast to former reports, these authors discovered various intestinal contents in different species of Mononchina, including *Clarkus papillatus* (Bastian, 1865) Jairajpuri, 1970. In addition to animal prey, their gut contents were composed of bacteria, actinomycetes and clay particles. So these predators played a role at three levels in foodwebs : predation, scattering and regulation of bacterial or fungal elements and organo-mineral migrations (carriage and perhaps physical or enzymatic action on clay particles). These three aspects intervene in the processes of transformation of organic materials and consequently influence the formation and evolution of humus type. So, a better definition of the predator's diet presented an improvement in soil ecology studies.

Although *Clarkus papillatus* preferred fresh forest soils with mull acid humus, it was an ubiquitous species relative to the type of humus with a remarkable constancy (Arpin, 1985). The aim of this work was to examine through transmission electron microscopy, the ultrastructure of intestinal contents of this species and their change during digestion. Moreover, the electron microscopic observations allowed to study histological

features linked to the diet, such as the occurrence of lamellar systems and electron dense granules in the intestinal microvilli.

Material and methods

Two samplings were taken in September 1985 and in April 1986 in locations with three different humus types (acid mull, moder and dysmoder according to the definitions of Manil (1959) and Duchaufour (1977, 1980)* in the state forest of Orléans (Ingrannes sector) and in the state forest of Sénart.

FOREST OF ORLÉANS

Station 1 : Sessile oaks *(Quercus petraea)* 100-160 years old, mixed with some beeches *(Fagus silvatica)* and hornbeans *(Carpinus betulus),* aged 30-40 years and with a subcontinous carpet of brambles *(Rubus schleicheri).* The acid mull humus was composed of a virtually non-existent layer H on a clayey, muddy sandy horizon A11 with a pH of 4.6. At the surface there were many earthworm casts and in places some white rots (basidiomycetes).

Station 2 : Close to the Station 1, with a similar planting, but situated on a slightly raised soil composed of a moder humus with a thin layer H (0.5-1 cm) on a horizon A11 with a granulometry similar to that of station 1 but with a lower pH (3.9).

Station 3 : Sessile and pedonculate oaks *(Quercus robur)* 150-200 years old mixed with beeches aged 30-40 years. It was a dysmoder humus with a very thick layer H (10-15 cm) on a clayey and acid horizon A11 (pH = 3.6). White rots were numerous but earthworm casts were absent.

These three sampling stations had a temporary hydromorphy close to the surface (30 cm in March-April).

FOREST OF SÉNART

Both stations were situated alongside the south-eastern edge of the forest that was naturally well drained. The complex, leached soils without hydromorphic features had a muddy and then a clayed profile, probably lying on Sannosian millstone.

Station 4 : Sessile oaks (250-300 years old with coppice of limes *(Tilia cordifolia)* growing on an acid mull humus (pH of horizon A11 = 4.3).

Station 5 : This station was based about 20 m from the former inside the acid mull zone under the crown of an old oak (300 years old) without limes in the neighbourhood. The humus was a moder with a layer H (approximatively 1 cm thick) extended on an horizon A11 (pH = 3.9).

GENERAL PROCEDURES

Nematodes were collected in the upper 10 cm of the soil in September 1985 in all the stations and in April 1986 in the forest of Orléans only. The serious drought during spring 1986 obliged us not to include the two stations of the forest of Sénart; the mononchs, sensitive to water deficit, were not abundant enough (Arpin, 1976, 1985).

After a series of washings and sievings of the soil, nematodes were collected and assorted under a stereoscopic microscope. Only *Clarkus papillatus* females were studied here, the males being very rare. They were prepared for electron microscopy as follows : after a two-hour prefixation in a 2.5 % glutaraldehyde solution added with a millonig phosphate buffer at 7.5 pH, the nematodes were transferred into a 2 % Difco gelose according to Wright and Jones (1965), then fixed in osmiun tetroxide for one hour. After dehydratation in successive baths of ethanol (from 10 to 100 %) and propylene oxide, the specimens were embedded in Epon 812 and then polymerized for two days in an incubator at 60º.

Ultrathin sections (about 1 000) were taken at three levels of the intestine (anterior, mid-region and posterior intestine) in order to study the successive stages of digestion. These sections were placed on copper grids and covered with a protective membrane (Formvar at 3 %) and then contrasted with lead citrate (Reynolds, 1963) and uranyl acetate. Observations and photographs were taken with a transmission electron microscope Hitachi 600 at the National Muséum in Paris.

---

* In each soil, complex relations between parent rock, vegetation, pedoclimate and organisms imply that the energy introduced into a system obeys different modes of biochemical transformations resulting in the formation of humus types biologically, morphologically and chemically different. The morphological analysis of the organic horizons prior to chemical studies allows to define different humus types according to the number and the thickness of the layers, L (unbroken original plant material), F (broken plant remains more or less mixed with mesofauna fecal pellets), and H (fecal pellets) laying on the organo-mineral horizon Al. The mull humus (acid mull, earth-mull or calcic mull) have a L layer directly laying on the horizon Al with a rapid incorporation of litter due to a strong animal and bacterial activity of great diversity. With the increase of the acidity accompanied by a slow organic material decomposition, the L layer becomes thicker and the layers F and H appear specific to the humus moder, dysmoder (H layer thicker, strong decrease in fauna diversity and increase in fungal activity) and mod (the three layers L, F, H, are very thick as a result from litter decomposition without fauna but essentially fungal intervention).
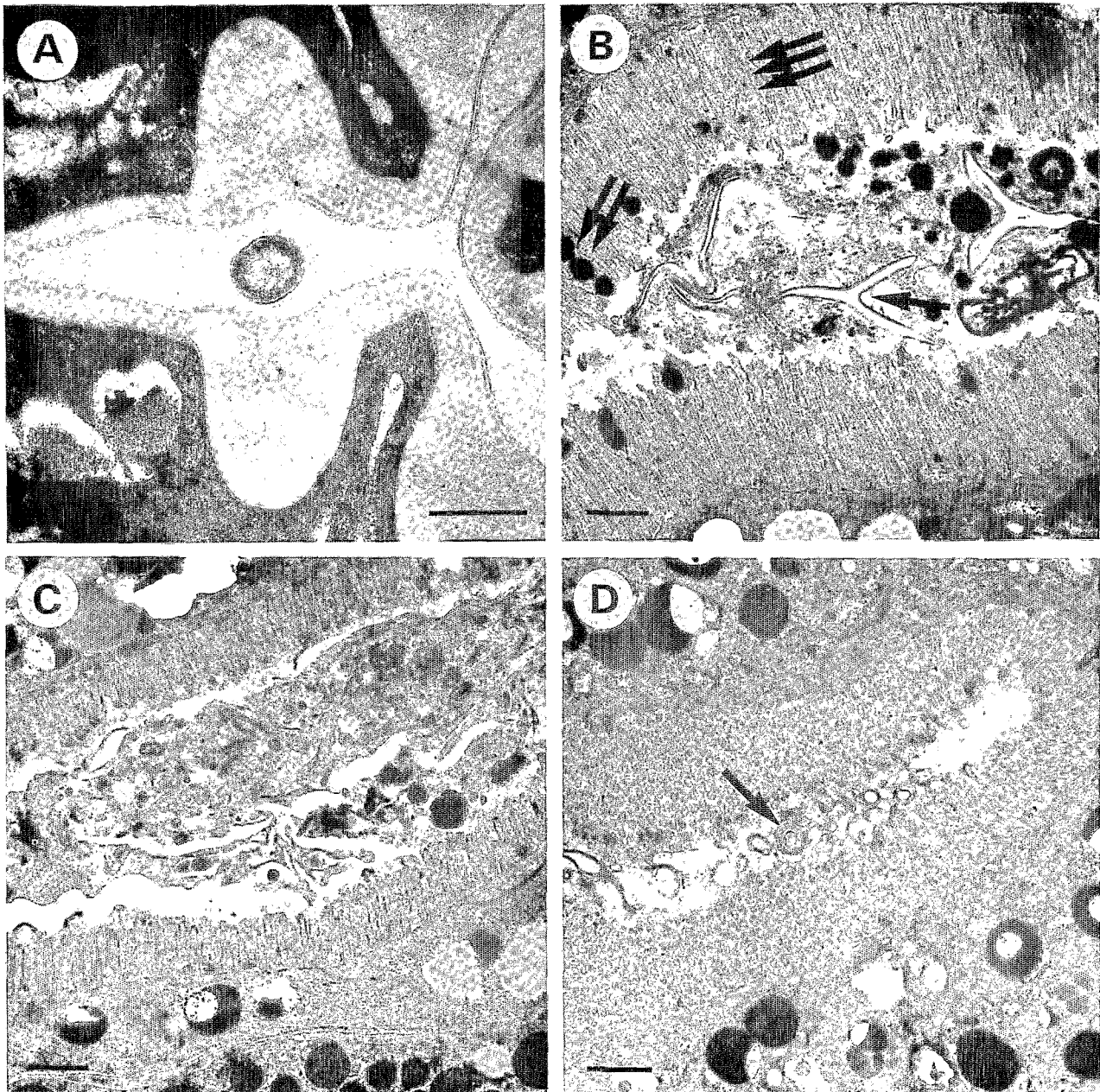
Fig. 1. Change of the intestinal content during digestion — A : Bacterium at level of oesophageal ampulla; B : Nematode oesophageal remains (arrow), electron dense granules (double arrow) and very long microvilli (triple arrow) at level of the anterior intestine; C : Cuticular remains, bacteria and shorter microvilli in the mid-intestinal region; D : Bacterial remains with figure of myelinization (arrow) in posterior intestine *(Bar = 1 μm).*

The spacial evolution of intestinal contents from sections of the same animal is shown in Figure 1 (A-D). We observed a bacterium at the level of an ampulla in the triradiate lumen of the oesophagus (Fig. 1 A). In the anterior intestine (Fig. 1 B) the microvilli are about

2.5 μm long. Cuticularized structures from animal tissues, as well as lamellar remains are visible; two structures with triradiate symmetry belonging to one or two nematodes are recognizable. Many electron dense granules occur among microvilli and in the digestive
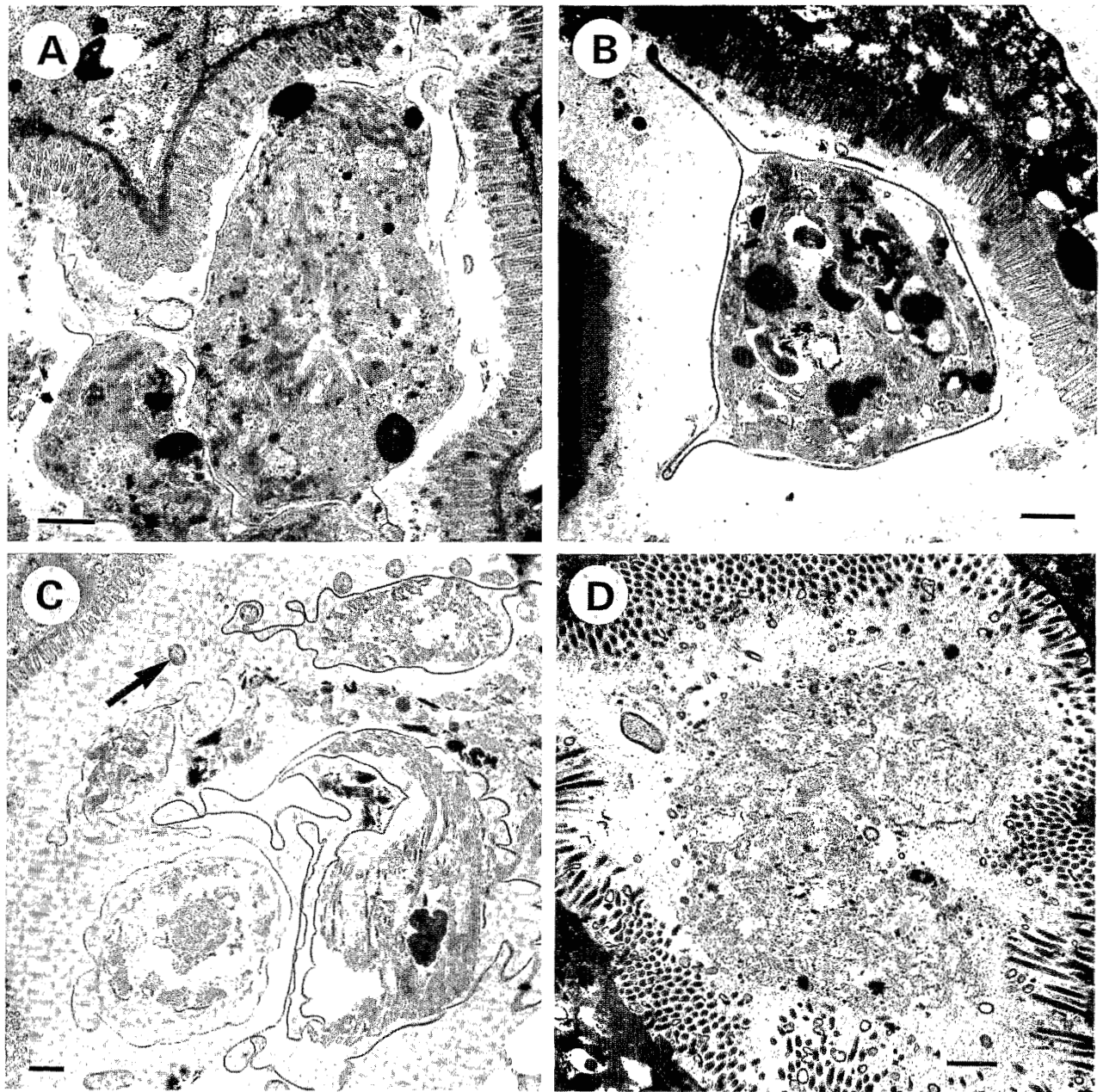
contents.

A more developed stage of digestion is shown in the mid-intestinal region (Fig. 1 C) though cuticular and lamellar remains of prey are still recognizable. Bacteria

are also present. Electron dense granules are less numerous than in the anterior intestine.

In the posterior intestine (Fig. 1 D), only unidentified lamellar fragments and figures of (bacterial?) myeliniza-

Fig. 2. Ingested prey — A : Section through nematode prey at level of oesophagus (a); B : Undetermined animal prey in mid-intestinal region and dense flocculent material among microvilli (a); C : Cuticular remains and bacteria (arrow) in midregion of intestine (a); D : Further digested animal and bacterial remains in posterior region of intestine with vesicular structures in contact with microvilli (b). *(Bar = 1 μm. Abbreviations for humus type, origin and date of collection : a = acid mull, Orléans, Sept. 1985; b = moder, Sénart, Sept. 1985; c = moder, Orléans, Sept. 1985.)*
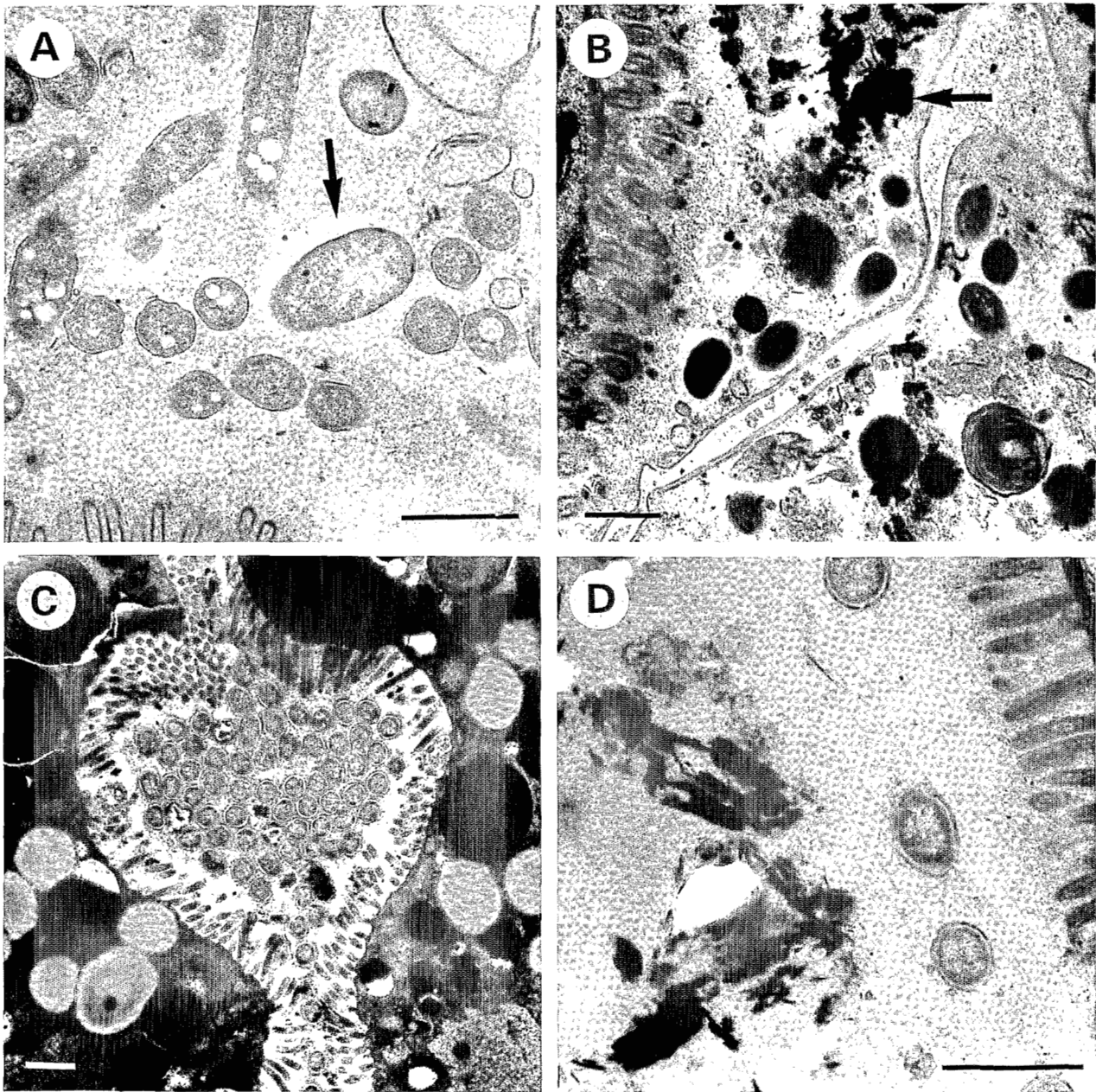
Fig. 3. Observation of microflora and clay particles — A : Bacterial activity in mid intestinal region with lytic zone (arrow) around some bacteria (c); B : Bacteria in contact with cuticular nematode remains in posterior intestine. Presence of clay particles (arrow) and figure of bacterial myelinization (a); C : Bacterial proliferation in posterior intestine (d); D : Clay particles in contact with bacteria (a). *(Bar = 1 µm. Abbreviations : see Fig. 2.)*

tion remain in the lumen. The size of intestinal microvilli is about 1.2 µm.

ANIMAL PREY

As shown above (Fig. 1 B) nematode remnants are recognizable in the intestine of *Clarkus papillatus*. Fig-

ure 2 A also shows a nematode previously swallowed and cut transversely with the triradiate symmetrical oesophagus in the centre. An unidentified animal prey can be observed in Figure 2 B with its cuticle and its internal tissues still quite well visible. At an earlier stage of digestion (Fig. 2 C) cuticular remains are still recognizable but internal tissues and cells are largely digested. In
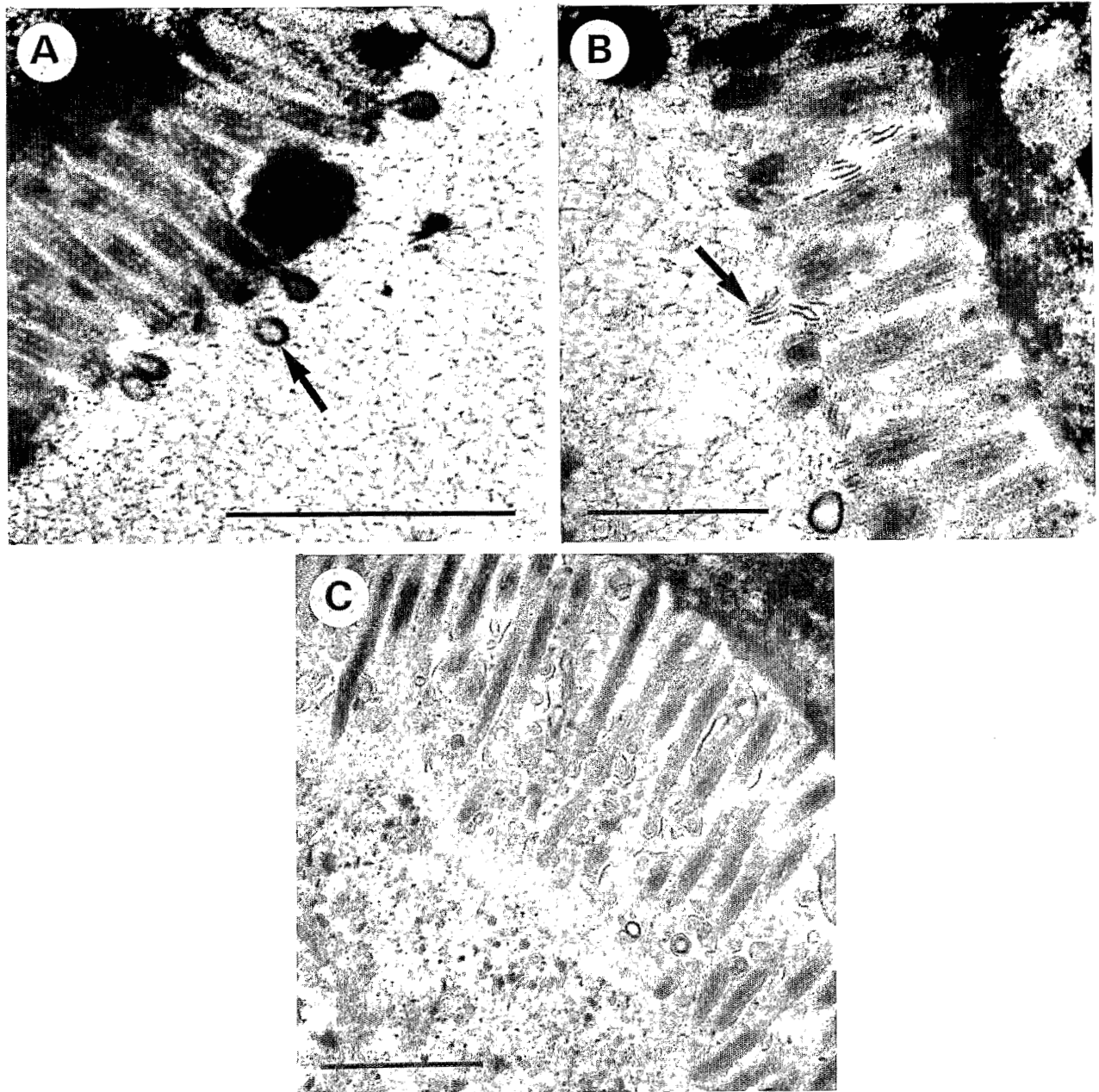
Fig. 4. Intestinal epithelium and histological aspects of digestive processes — A : Vesicular structures (arrow) at the end of microvilli in posterior intestine (b); B : Lamellar structures at level of mid intestinal region (a); C : Complex assemblage of lamellar and vesicular structures (c). *(Bar = 1 µm. Abbreviations : see Fig. 2.)*

the posterior intestine (Fig. 2 D) there is only a mass of food without an identifiable structure. At this stage of digestion, electron dense flocculent material, most likely secreted by epithelial cells and present throughout the intestine, is more abundant and fills the lumen. More anteriorly it is denser close to the microvilli (Fig. 2 B). At the ultimate stage of digestion numerous vesicles are in contact with intestinal microvilli (Fig. 2 D).

MICROFLORA AND CLAY PARTICLES

Ingestion of bacteria by *Clarkus papillatus* is shown in Figure 1 A, a section through the oesophagus, where a bacterium is visible in one of the three oesophageal ampulla. Figures 3 A, 3 B and 3 C indicate the presence of active bacterial colonies at different levels of the intestine. A bright zone around some bacteria can be observed that corresponds to the lysis of electron dense flocculent material in the intestinal lumen (Fig. 3 A & 3 B). These bacteria in the alimentary canal are generally in contact with the alimentary bolus and situated at its periphery. They can, however, be included in the digestive contents in close contact with cuticular remains (Fig. 3 B) and clay particles (Fig. 3 B & 3 D). Figure 3 B also shows the myelinization of a bacterium (also refer to Fig. 1 D concerning digestion of bacteria). Moreover, we observed a proliferation of bacteria in the intestine (Fig. 3 C).

HISTOLOGICAL ASPECTS OF DIGESTIVE PROCESSES

Figures 4 A and B show the electron dense flocculent material most likely secreted by the intestinal epithelium (Ohkura, 1976). This material forms networks surrounding alimentary particles in the intestinal lumen (see also Figs 2 D, 3 A, 3 D). The lumen always contained these products.

Electron dense granules, about 0.3 μm in diameter, occur among microvilli (Fig. 1 B). Others are in the intestinal lumen (Fig. 4 A) or in digestive contents (Figs 1 B, C). These granules seem to be especially abundant in the anterior intestine and mid-intestinal region of *Clarkus papillatus*.

In addition, lamellar (Fig. 4 B) and vesicular (Fig. 4 A), structures or complex assemblages of the two structures (Fig. 4 C) appear at the end of microvilli or among them. The lamellar structures are essentially observed in the mid-region of the intestine in contrast to vesicles which appear in the posterior region. The lamellar structures seem to be parallel to microvilli and often in their extension. Their membranes are composed of double lamina.

Discussion

The electron microscopic study carried out at three levels of the intestine offered information and hypotheses about some histological features connected with feeding.

Electron dense flocculent material which always lined the wall of the intestine and formed networks in the lumen, consists probably of muco-proteins and muco-polysaccharides (Bennet, 1963; Jenkins & Erasmus, 1969). The electron dense granules among microvilli and lamellar and vesicular structures may be interpreted in view of their formation and localization.

Dense globular elements principally appeared in the anterior intestine and partly in the mid-region of the intestine, lamellar structures were essentially confined to the mid-region, whereas vesicles were mainly observed in the posterior intestine. It was interesting to compare the localization of these elements in the lumen with those inside the epithelium cells. Bird (1971) pointed out that several species of animal parasitic nematodes contained dense granules and lamellar bodies (compared to lysosoma) in epithelial cells in the anterior intestine and mid-region of the intestine. It may be supposed that these structures observed in *Clarkus papillatus*, either in this work or in a former survey (Arpin & Kilbertus, 1981), as well as in other nematodes reported were secreted by the intestinal epithelium cells (Shepherd & Clark, 1976; King, 1982; Nuss, 1985). Nevertheless we should point out that the lamellar structures described by Nuss (1985) had a membrane with only one lamella whereas our observations revealed double lamella membranes. These lamellae were situated perpendicularly or in a parallel direction to microvilli and to their extension. Nevertheless, they could also be scattered in the lumen and sometimes could surround bacteria (Nuss, 1985).

The role of these lamellar and vesicular structures is still questioned : the observations of Nuss (1985) allow to suggest a probable part in the adsorption of bacteriolytic enzymes, but it could also be an origin of muco-substances. For collembola (Humbert, 1979) and the grasshopper *Locusta migratoria* (Heinrich & Zebe, 1973), a relation between these vesicular structures and the different stages of digestion was strongly suggested. Different studies on animal parasitic nematodes seemed to prove that the anterior intestine has a secretory activity, whereas the posterior intestine plays rather a role in absorption (Enigk, 1938; Carpenter, 1952; Lee, 1968; Lee & Miller, 1969). So in *Clarkus papillatus,* the presence of electron dense granules in great number in the anterior intestine may be explained as an enzymatic secretion. The vesicular structures in the posterior intestine may be explained as products of apocrine secretion.

The lamellar structure observed in the mid-intestinal region did not appear in all sections. So they could be linked to stages of digestion or to physiological conditions of the animal (renewal of microvilli). Considering the high level of variability of these secretions, more abundant material and regular samplings over the year could allow a determination of these phenomena.

Concerning the diet of adult *Clarkus papillatus*, this survey, confirming previous observations, underlines the variety of food items.

Ingestion and digestion of animal prey (nematodes and unknown organisms) confirm the predatory behaviour of this species as defined by some authors from light microscope observations (Cobb, 1913; Steiner & Heinly, 1922; Thorne, 1927; Bilgrami, Ahmad & Jairajpuri, 1986). This species does not only suck up the liquefied contents of the prey as do other mononchids

such as *Mylonchulus* (Cohn & Mordechai, 1974; Mo-
handas & Prabhoo, 1980), but also swallows it wholly or
by pieces. Arpin and Kilbertus (1981) dit not discover
animal remains in their observations of alimentary tract
sections of *Clarkus papillatus* by transmission electron
microscopy. The present survey shows that only the
anterior or mid-intestinal region allows without any
doubt the identification of ingested prey. The gradual
change of this material during the intestinal process was
interesting to analyse, especially as the absence of cuti-
cular remains in the posterior intestine became evident.
We suggest that this results from a complete digestion of
the prey. This is probably not a general phenomenon in
mononchids that ingest entire prey because Mulvey
(1961) pointed out the expulsion of cuticule through the
anus in *Anatonchus* sp.

This study also permitted information on microflora
observed in the alimentary tract of *Clarkus papillatus*.
The bacteria may have a dual function. On the one hand,
they may be used as food as the observations of remains
suggested. Figures of myelinization also indicate the
digestion of bacteria. On the other hand some obviously
viable bacteria persisted in the intestine. The presence of
a lytic zone around bacteria expressed their active part in
digestion.

The bacteria observed in the intestine have been
ingested directly from colonies or microbial aggregates
in the soil. However, several negatives similar to Figure
3 C suggested a multiplication of bacteria inside the
alimentary canal. This proliferation cannot be explained
simply by food ingested (the concentration of germs is
too high) or by an infection (the surrounding tissues did
not show any sign of infestation). It is, however, imposs-
ible to judge whether the same germs were digested and
also active and if they all came from the soil. A non
published study related to isolation and culture of in-
testinal microflora of *Clarkus Papillatus* (60 females
from station 1, in Spring 1986) showed that the germs
are represented by both common soil and litter species
(Bacillus subtilis and *Pseudomonas cepacia)* and by an
unknown species which did not live in the soil. This
unknown species could be strictly an intestinal bac-
terium. The two common soil bacteria are known to
intervene in diverse enzymatic processes, in particular
proteolysis (Waksman, 1952; Pochon & de Barjac, 1958).

From a strict ecological point of view, this work seems
to confirm the intervention of *Clarkus papillatus* at three
levels in foodwebs. First, at the carnivorous level
because this mononch is a real predatory species. Second
at the microbivorous level because this species might
intervene, as other soil microfauna animals (particulary
the bacteriophagous nematodes), on grazzeing, scatter-
ing and regulating bacterial population. Notably the
observation of digested bacteria confirms the possibility
to culture successfully *Clarkus papillatus* on soil decoc-
tion enriched with soil bacteria and colloidal particles
without other animal prey (Arpin, 1976). This diet seems

fundamental for newly hatched juveniles, still inapt for
predation (Steiner & Heinly, 1922; Overgaard - Nielsen,
1949). Futhermore, the presence of active bacteria and
a multiplication of germs in the intestine may suggest a
symbiotic relation, but also the possibility of expulsion
of viable bacteria through the anus and its scattering in
the soil. This last aspect must be associated with the
carriage and the scattering of clay particles by *Clarkus
papillatus*. This organo-mineral part which was not
included in the diagram structure of the saprophagous
system of Heal and Maclean (1975), has a great role in
the transformation of litters : the presence of these clays
on leaves considerably increases the activity of biode-
gradation by the bacterial microflora (Touchot, Kilber-
tus & Vannier, 1983; Touchot, 1984). These organo-
clayey mixings, favourable to bacterial development, and
largely due to integration of mineral elements in the
alimentary bolus of different soil animals such as col-
lembola (Vannier & Kilbertus, 1981) or nematoda (Ar-
pin & Kilbertus, 1981) can be traced in soils as micro-
agregates (Arpin *et al.,* 1980). Kilbertus and Vannier
(1981) have shown the importance of clay ingestion by
Tomocerus problematicus, an obligate cave-dwelling col-
lembole : clay is absolutely required for the growth of
this species. Further work is needed to determine the
role of these clayey particles in the diet of *Clarkus
papillatus*. Although the available specimens did not
allow a strict quantitative study (only 24 females have
been observed at three levels of the intestine, each with
about ten sections or more) we noticed that clay particles
were only present in animals collected from mull humus
as in a previous study (Arpin & Kilbertus, 1981).
Animals extracted from moder or dysmoder did not
contain clay particles.

This TEM survey presents results from observations
at two seasons of the year. It seemed that prey is present
in the intestine of pratically all animals collected in
September 1985 (9 out of 12) whereas in April 1986 the
number was lower (5 out of 12). Further work is needed
to propose an hypothesis on the diversification of the
diet of *Clarkus papillatus,* relative to humus type and
season, which might correspond to an adaptative nutri-
tional behaviour : Maximal abundance and reproduc-
tion of this species in autumn and winter (Arpin, 1985)
when animals have a bigger size (Arpin, Jagers op
Akkerhuis & Ponge, 1988) could be partly linked to a
carnivorous diet. Without disregarding the influence of
physical and chemical factors, these nutritional aspects
must be considered to determine the place and role of
Clarkus papillatus in soil system ecology.

REFERENCES

ARPIN, P. (1976). Étude et discussion sur un milieu de culture pour Mononchidae. *Revue Écol. Biol. Sol.*, 13 : 629-634.

ARPIN, P. (1985). *Les nématodes libres indicateurs de la nature et de l'évolution des humus forestiers.* Thèse Doctorat d'État, Université Pierre et Marie Curie, Paris VI, 200 p.

ARPIN, P., JAGERS OP AKKERHUIS, G. & PONGE, J. F. (1988). Morphometric variability in *Clarkus papillatus* (Bastian, 1865) Jairajpuri, 1970 in relation to humus type and season. *Revue Nématol.*, 11 : 149-158.

ARPIN, P. & KILBERTUS, G. (1981). Ultrastructure du contenu digestif et de l'épithélium intestinal chez quelques nématodes prédateurs (Mononchida) et bactériophages. *Revue Nématol.*, 4 : 131-143.

ARPIN, P. KILBERTUS, G., PONGE, J. F. & VANNIER, G. (1980). Importance de la microflore et de la microfaune en milieu forestier. In Pesson, P. (Ed.) *Actualités d'écologie forestière.* Paris, Gauthier-Villars : 87-150.

AZMI, M. I. (1983). Predatory behaviour of nematodes. 1. Biological control of *Helicotylenchus dihystera* through the predaceous nematode *Iotonchus monhystera. Indian J. Nematol.*, 13 : 1-8.

BENNET, H. S. (1963). Morphological aspects of extracellular polysaccharides. *J. Histochem. Cytochem.*, 11 : 14-23.

BILGRAMI, A. L., AHMAD, I. & JAIRAJPURI, M. S. (1986). A study of the intestinal contents of some mononchs. *Revue Nématol.*, 9 : 191-194.

BIRD, A. F. (1971). *The structure of nematodes.* New York, Academic Press, 318 p.

CARPENTER, M. F. P. (1952). The digestive enzymes of *Ascaris lumbricoides* var. *suis*, their properties and distribution in the alimentary canal. *Dissert. Univ. Michigan*, 399 p.

COBB, N. A. (1913). Notes on *Mononchus* and *Tylenchulus. J. Wash. Acad. Sci.*, 10 : 287-288.

COHN, E. & MORDECHAI, M. (1974). Experiments in suppressing citrus nematode populations by use of a marigold and a predacious nematode. *Nematol. medit.*, 2 : 43-53.

DUCHAUFOUR, P. (1977). *Pédologie. 1. Pédogénèse et classification.* Paris, Masson, 477 p.

DUCHAUFOUR, P. (1980). Écologie de l'humification et pédogénèse des sols forestiers. In Pesson, P. (Éd.) *Actualités d'écologie forestière*, Paris, Gauthier-Villars : 177-203.

ENIGK, K. (1938). Ein Beitrag zur Physiologie und zum Wirt-parasit-verhältnis von *Graphidium strigosum. Z. Parasitenk.*, 10 : 386-414.

HEAL, O. W. & MACLEAN, S. F. (1975). Comparative productivity in ecosystems-secondary productivity. In Van Dobben, V. H. & Lowe-Mac-Connell, R. H. (Eds) *Unifying concepts in Ecology*, The Hague, Junk : 89-108.

HEINRICH, D. & ZEBE, E. (1973). Zur Feinstruktur der Mitteldarmzellen von *Locusta migratoria* in verschiedenen Phasen der Verdauung. *Cytobiologie*, 7 : 315-326.

HUMBERT, W. (1979). *Les organes des collemboles : étude ultrastructurale, cytochimique, spectrographique et approche*

écologique. Thèse de Doctorat d'État, Université de Strasbourg, 167 p.

JENKINS, T. & ERASMUS, D. A. (1969). The ultrastructure of the intestinal epithelium of *Metastrongylus* sp. *Parasitology*, 59 : 335-342.

KILBERTUS, G. & VANNIER, G. (1981). Relations microflore-microfaune dans la grotte de Sainte-Catherine (Pyrénées ariégeoises). II. Le régime alimentaire de *Tomocerus minor* (Lubbock) et *Tomocerus problematicus* Cassagnau (Insectes collemboles). *Revue Écol. Biol. Sol*, 18 : 319-338.

KING, T. P. (1982). An extracellular lamellar system associated with the luminal surface of intestinal microvilli in the marine nematode *Enoplus communis. Nematologica*, 28 : 156.

LEE, D. L. (1968). The ultrastructure of the alimentary tract of the skin-penetrating larva of *Nippostrongylus brasiliensis. J. Zool. Lond.*, 154 : 9-18.

LEE, C. C. & MILLER, J. H. (1969). Fine structure of the intestinal epithelium of *Dirofilaria immitis* and changes occurring of the vermicidal treatment with caparsalate sodium. *J. Parasitol.*, 55 : 1035-1045.

MANIL, G. (1959). Aspects pédologiques du problème de la classification des sols forestiers. *Pedologia*, 9 : 124-226.

MOHANDAS, C. & PRABHOO, N. R. (1980). The feeding behaviour and food preferences of predatory nematodes Mononchida from the soils of Kerala (India). *Revue Écol. Biol. Sol*, 17 : 53-60.

MULVEY, R. H. (1961). The Mononchidae : a family of predaceous nematodes. I. Genus *Mylonchulus. Can. J. Zool.*, 39 : 665-696.

NUSS, B. (1985). Ultrastrukturuntersuchungen zur Nährungsabsorption von aquatischen Nematoden. *Verhoeff. Inst. Meeresforsch. Bremerh.*, 21 : 1-69.

OHKURA, T. (1976). Ultrahistochemical observations of the cell surfaces with special reference to the localization of muco-substances. *Acta Histochem. Cytochem.*, 9 : 46-51.

OVERGAARD-NIELSEN, C. (1949). Studies on the soil micro-fauna. II. The soil-inhabiting nematodes. *Natura Jutlandica*, 2 : 1-131.

POCHON, J. & de BARJAC, H. (1958). *Traité de microbiologie des sols.* Paris, Dunod, 685 p.

REYNOLDS, E. S. (1963). The use of lead citrate at high pH as an electron-opaque stain in electron microscopy. *J. Cell. Biol.*, 17 : 208-212.

SHEPHERD, A. & CLARK, S. A. (1976). Structure of the anterior alimentary tract of the passively feeding nematode *Hexatylus viviparus. Nematologica*, 22 : 332-342.

SMALL, R. W. (1979). The effects of predatory nematodes on populations of plant parasitic nematodes in pots. *Nematologica*, 25 : 94-103.

SMALL, R. W. (1987). A review of the prey of predatory soil nematodes. *Pedobiologia*, 30 : 179-206.

STEINER, G. & HEINLY, H. (1922). The possibility of control of *Heterodera radicicola* and other plant-injurious nemas by means of predatory nemas, especially by *Mononchus papillatus. J. Wash. Acad. Sci.*, 12 : 367-386.

THORNE, G. (1927). The life history, habits and economic importance of some Mononchs. *J. agric. Res.*, 34 : 265-286.

TOUCHOT, F. (1984). *Relation microflore-microfaune dans le cadre de la biodégration des écorces et des litières.* Thèse 3e cycle, Université de Nancy I, 221 p.

TOUCHOT, F., KILBERTUS, G. & VANNIER, G. (1983). Rôle d'un collembole *(Folsomia candida)* au cours de la dégradation des litières de charme et de chêne, en présence ou en absence d'argile. In P. Lebrun *et al.* (Eds) *New trends in soil biology,* Proc. 8th int. Colloq. Soil. Zool. : 269-280.

VANNIER, G. & KILBERTUS, G. (1981). Participation des insectes collemboles et des microorganismes telluriques aux processus de migration des substances organo-minérales. In *Migrations organo-minérales dans les sols tempérés,* Coll. int. C.N.R.S. n° 303, Nancy, sept. 1979. Paris Éd. CNRS : 133-144.

WAKSMAN, S. A. (1952). *Soil microbiology.* New York, Wiley & Sons, 356 p.

WRIGHT, K. A. & JONES, N. O. (1965). Some techniques for the orientation and embedding of nematodes for electron microscopy. *Nematologica,* 11 : 125-130.