A myxozoan-like parasite causing xenomas in the brain of the mole, *Talpa europaea* L., 1758 (Vertebrata, Mammalia)

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SUMMARY

Light and transmission electron microscopy revealed pericytes of brain capillaries of moles (*Talpa europaea* L., 1758) as parasitized intracellularly. These host cells were enlarged and of globular or ellipsoid shape, and incorporated a cell-within-cell sequence of primary, secondary and, rarely found, tertiary developmental stages of an eukaryotic organism. Other stages like spores were not discovered either in brain or in other organs. Due to the vertebrate host, and the parasitic cells showing the enveloped state this parasite can be classified as belonging to the Myxozoa rather than Paramyxea. Since spores, which would allow an exact identification of the parasite, could not be detected and mammals are very unusual hosts for Myxozoa, the parasite was designated a myxozoan-like organism.

Key words: myxozoan-like organism, brain xenomas, *Talpa europaea*, ultrastructure.

INTRODUCTION

The enveloped state, which is the presence of cells within cells, is characteristic of 2 phyla, Myxozoa (Lom, 1990) and Paramyxea (Desportes & Perkins, 1990). Both are microscopic parasites forming multicellular spores and, in some cases, they are associated with xenomas, which are enlarged intracellularly parasitized host cells.

Myxozoa have been detected in platyhelminths (Overstreet, 1976; Siau, Gasc & Maillard, 1981), bryozoa (Canning, Okamura & Curry, 1996; Okamura, 1996), annelids (Jirovec, 1940; Lom, Yokoyama & Dykova, 1997; Bartholomew *et al*. 1997), fishes (El-Matbouli & Hoffman, 1996; Sitja-Bobadilla & Alvarez-Pellitero, 1995; Lom *et al*. 1989), amphibians (Chakravarty, 1940; Desser, Lom & Dykova, 1986; Upton *et al*. 1992; Upton, McAllister & Trauth, 1995; Hill, Green & Lucke, 1997) and reptiles (Chakravarty, 1940; Johnson, 1969). Some of the myxozoan species known from fishes seem to be harmless (Masoumian, Baska & Molnar, 1994; Roubal, 1994; Morado & Sparks, 1986; Masoumian, Baska & Molnar, 1996), and others cause great damage (Plehn, 1905; Keysselitz, 1908; Alvarez-Pellitero & Sitja-Bobadilla, 1993). Obligate alternating host changes between fish (myxosporean phase of the life-cycle) and annelids (actinosporean phase), have been described for several myxozoan species (Wolf & Markiw, 1984; El-Matbouli & Hoffmann, 1989; Yokoyama, Ogawa & Wakabayashi, 1995; Bartholomew *et al*. 1997). This might not be a general rule for all Myxozoa because there is a report of successful experimental infection of fish using myxosporean spores without involvement of actinosporeans (Diamant, 1997). Paramyxea have been found in annelids (Chatton, 1911; Desportes, 1981), arthropods (Ginsburger-Vogel & Desportes, 1979*a*, *b*) and molluscs (Perkins, 1976; Perkins & Wolf, 1976).

To date neither Myxozoa nor Paramyxea have been observed parasitizing homoiothermic vertebrates. This paper is the first record of putative myxozoan or paramyxean life-cycle stages living in a mammal host.

MATERIALS AND METHODS

Fifty-five moles (*Talpa europaea*) were trapped from 1982 to 1985, and in 1994 near Graz (Styria, Austria), covering every month of the year. The specimens were dissected and processed for light and electron microscopy.

Smears were made from brain, spinal cord and blood; freshly dissected pieces of liver, kidneys, heart, muscles and guts were pressed onto slides. Both kinds of preparations were fixed with methanol,

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† Professor Dr Otto Kepka who was greatly engaged in this work died in 1996.

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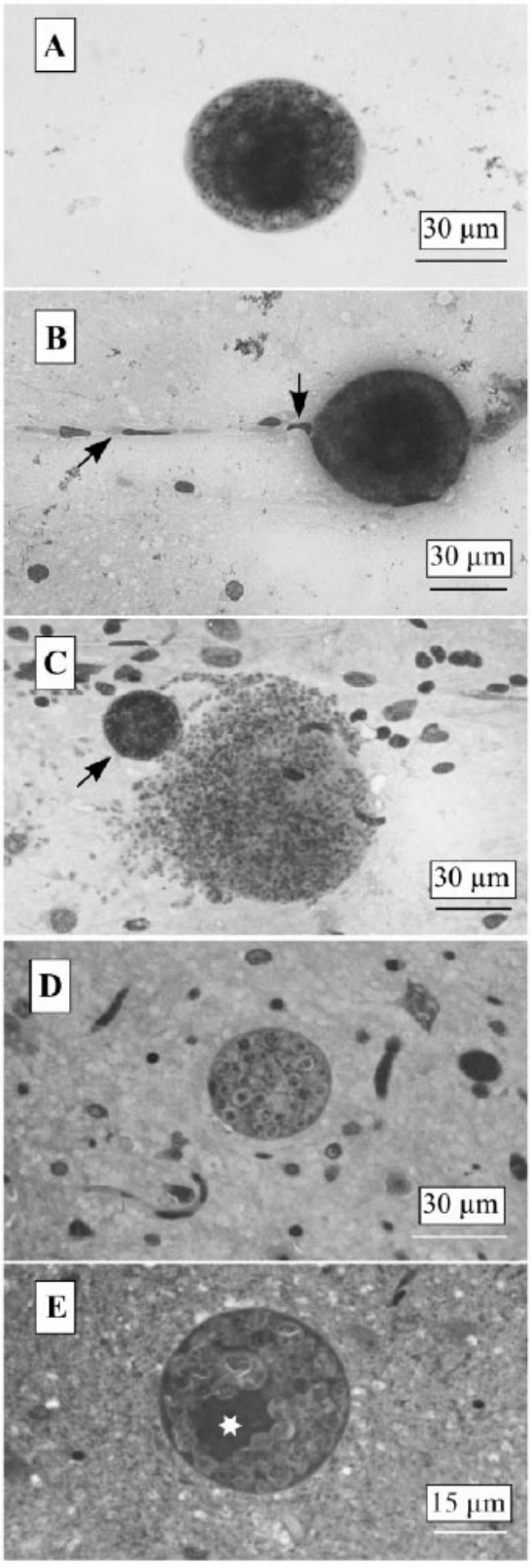

Fig. 1. Light microscopic photographs of the myxozoan-like organism found in brains of *Talpa europaea*. (A–C) Giemsa-stained smears. (D–E) Toluidine blue stained semi-thin sections. (A) Ellipsoid xenoma. (B) The xenoma is connected with a blood capillary (arrows). (C) Burst xenoma, the enlarged host cell nucleus (arrow) near the destroyed xenoma shows a rather smooth surface. (D) Peripheral section of a xenoma. (E) Central section of a xenoma showing the host cell nucleus (asterisk) deformed by the parasitic stages.

stained with Giemsa's stain and examined for parasites. Small pieces of infected tissue were fixed in 3 % glutaraldehyde in 0·2 M cacodylate buffer (pH 7·2) for 24 h. After washing in cacodylate buffer and post-fixation in 1 % OsO_4 in the same buffer, the tissue pieces were embedded in Epon or Spurr. Semi-thin sections were stained with toluidine blue. After discovery of parasites in semi-thin sections, ultra-thin sections from 60 xenomas were stained with uranyl acetate and lead citrate and examined with a Zeiss EM 9 and a Philips 300.

Xenomas found in brain smears were measured and classified according to their shape as globular or ellipsoid. They were considered as ellipsoid if their rectangular diameters differed by more than 2·5 μm which corresponded to 1 graduation mark on the Reichert light microscope at the magnification used.

Series of photographs from ultra-thin sections of parasitic stages were obtained and processed by image analysis (OPTIMAS) techniques. The stages were marked by interactively tracing their boundaries. The directions and positions of the individual units were adjusted by translatory and rotatory corrections. This was achieved on the basis of an optimum match of the identified units between consecutive sections.

RESULTS

Hosts

From a total of 55 moles with body weights between 190 and 290 g and total lengths between 13·5 cm and 16·0 cm, 30 specimens (54·54 %) contained xenomas in their brains, caused by life-cycle stages of a putative myxozoan or paramyxean organism. Both sexes were parasitized in similar quantity (14 females, 16 males). None of the other investigated organs and tissues showed any stages of the same type of parasite.

Light microscopy

In most brains of infected moles, xenomas (Fig. 1A–E) were rare and therefore difficult to find. However, they were distributed all over the brains, often next to capillaries (Fig. 1B). They showed a distinct, homogeneous membrane which proved to be extremely resistant against the mechanical pressure caused by smearing the brain sample between 2 slides; only few parasitized cells burst during that procedure (Fig. 1C). The host cell nucleus within xenomas looked star-shaped. The space between the nucleus and the outer limiting membrane was filled

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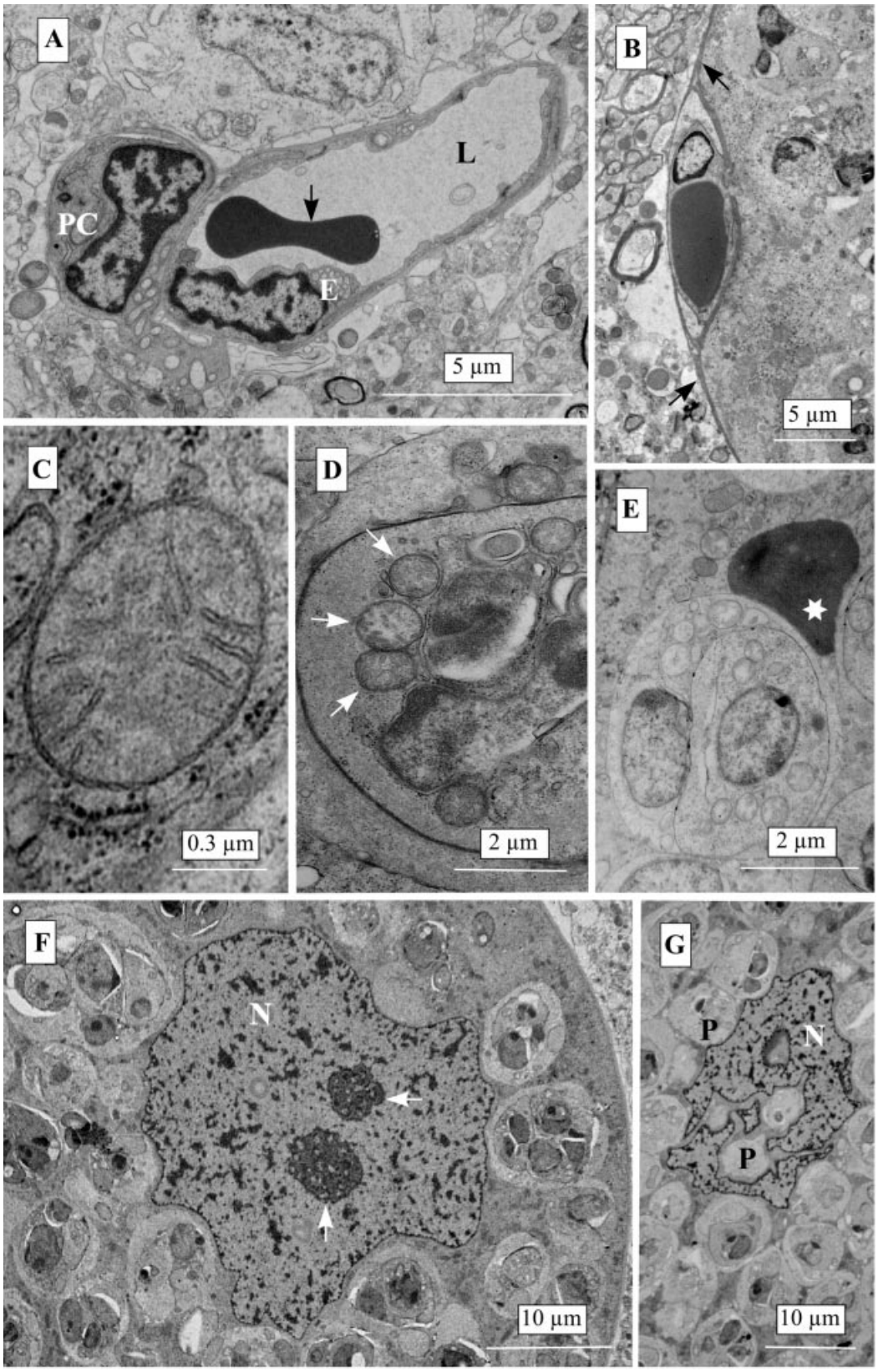

Fig. 2. Transmission electron microscopic images of host cell, xenoma and parasitic stages. (A) Section of a blood capillary. The lumen (L) of the blood vessel shows an erythrocyte (arrow). There are also an endothelial cell (E) and a non-parasitized pericyte (PC). (B) The xenoma is surrounded by the basic lamina (arrows) of the capillary. (C) The host cell mitochondrion is of the cristae-type. (D) The mitochondria (arrows) of the parasitic stages are of the tubular type. (E) There are often accumulations of electron-dense material (asterisk) between parasitic stages. (F) The enlarged host cell nucleus (N) shows 2 nucleoli (arrows). (G) The irregular shape of the host cell nucleus (N) is caused by parasitic stages (P).

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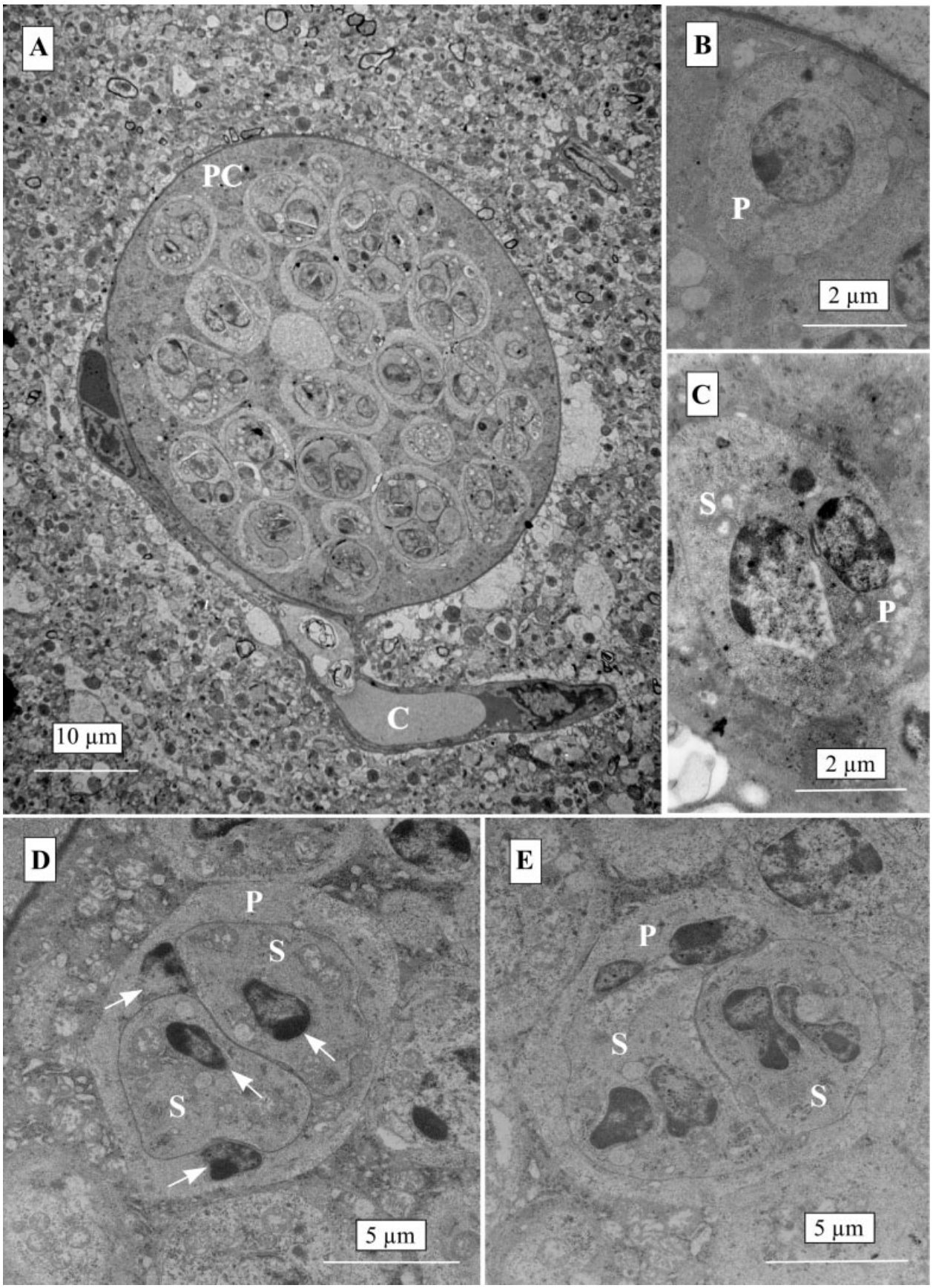

Fig. 3. Transmission electron microscopic images of parasitic stages found in brains of *Talpa europaea*. (A) The pericyte (PC) of the blood capillary (C) is filled with different parasitic stages. (B) Section of a primary cell (P). (C) The earliest parasitic stage found within the moles' xenomas consists of a primary cell (P) containing a secondary cell (S). (D) A binucleate primary cell (P) contains 2 mononucleate secondary cells (S). Nuclei are marked by arrows. (E) The primary cell (P) contains 2 binucleate secondary cells (S).

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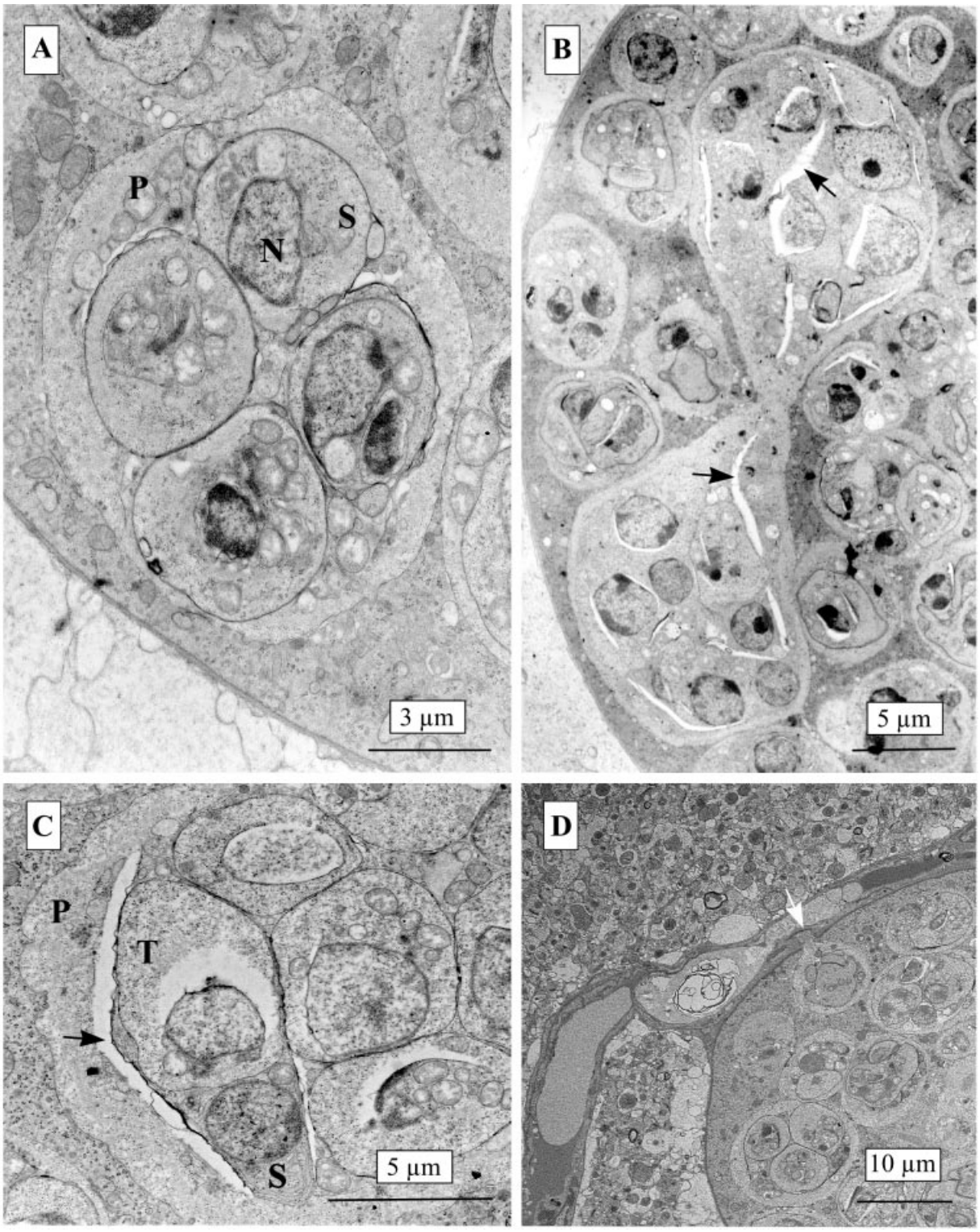

Fig. 4. Transmission electron microscopic images of parasitic stages found in brains of *Talpa europaea*. (A) A primary cell (P) contains 4 mononucleate (N, nucleus) secondary cells (S). (B) Giant stages (in this case a dumbbell-shaped section) occur rarely in xenomas. These stages always showed shrinkage fissures (arrows). (C) Only few secondary cells (S) of giant stages (P, primary cell) contain a tertiary cell (T). The arrow marks a shrinkage fissure. (D) A parasitic stage seems to leave (arrow) the xenoma.

with globular or ellipsoid parasitic bodies, each provided with 1 or more nuclei. The dents of the host cell nucleus seem to be caused by the high packing density of parasites (Fig. 1E). In only 2 of the preparations isolated nuclei of burst xenomas were found. They showed smooth membranes without dents. One of them was globular with a diameter of 30·0 μm, the other was ellipsoid with

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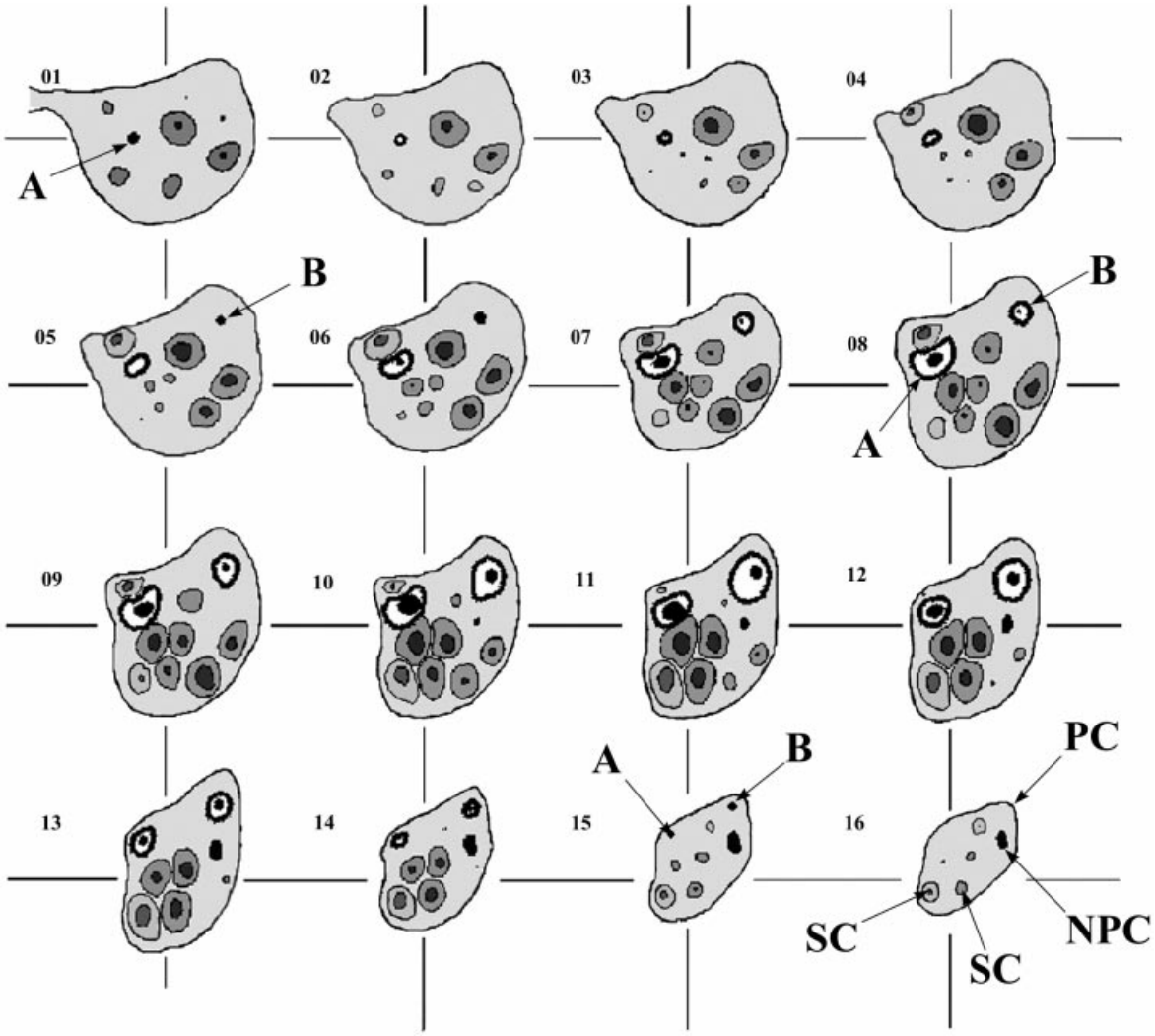

Fig. 5. Series of available matching ultrathin sections of a part of a giant stage of the myxozoan-like organism found in a brain xenoma of *Talpa europaea*. A primary cell (PC) with 1 nucleus (NPC) contains many mononucleate secondary cells (SC). Two of these secondary cells (A and B) can be followed through the images of the series of sections.

diameters of 22·5 μm and 15·0 μm. In total, 277 xenomas from smears were measured. The means and standard deviations of the diameters of the xenomas were $56{\cdot}9 \pm 7{\cdot}6$ μm (max. 75·0 μm, min. 45·0 μm) for the globular type, and $60{\cdot}3 \pm 9{\cdot}7$ μm (max. 102·5 μm, min. 35·0 μm) by $52{\cdot}0 \pm 8{\cdot}1$ μm (max. 67·5 μm, min. 32·5 μm) for the ellipsoid type.

Ultrastructure

All host cells were pericytes (Figs 2A and 3A) of capillaries. In transverse sections of capillaries, the few uninfected pericytes, which had been identified in the preparations, had a maximum dimension of $5{\cdot}5 \times 3{\cdot}5$ μm omitting the thin appendices of the cellular bodies. The irregularly shaped nuclei of uninfected pericytes were $5{\cdot}0 \times 3{\cdot}0$ μm maximum. The basal lamina of the capillary surrounding the host cells varied considerably in thickness: in uninfected pericytes it was 40–80 nm, and in parasitized pericytes 60–200 nm (Fig. 2B). Pericytes and their parasites contained mitochondria of different types. Host cell mitochondria were of the cristae-type (Fig. 2C), while those of the parasitic stages were of the tubular type (Fig. 2D). The cytoplasm of the parasitized host cells also showed accumulations of fine-grained electron-dense material interspersed by less electron-dense inclusions (Fig. 2E). The hypertrophied nuclei of the parasitized host cells often harboured 1 or 2 nucleoli (Fig. 2F). The marginal regions of these nuclei showed fissures as a result of the dense packing of the parasitic stages (Fig. 2G).

The xenomas contained different developmental stages of the parasite (Fig. 3A): the earliest stage, found in one plane of an ultra-thin section, appeared

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as a single cell with 1 nucleus (Fig. 3B), but in tracking the subsequent sections this cell turned out to be a mononucleate primary cell containing also 1 mononucleate secondary cell (Fig. 3C). The nuclei of the primary cells of these stages in most cases were globular or ellipsoid and sometimes U-shaped. The next distinguishable stage consisted of a primary cell showing 1 or 2 separate nuclei and 2 mononucleate secondary cells (Fig. 3D). The following step in development led to the division of each secondary cell nucleus, resulting in binucleate secondary cells (Fig. 3E). Most frequent in our preparations were primary cells with 4 secondary cells (Fig. 4A). It was not possible in ultra-thin sections to determine the number of nuclei, especially of the primary cells of these stages. A few xenomas from moles caught in spring and autumn contained sporadic giant stages (Fig. 4B). Unfortunately they always showed marks of insufficient fixation and infiltration of embedding material. Some of them were rather ellipsoid, some were vermiform and showed constrictions. They were composed of very large primary cells and a great number of secondary cells (Fig. 5). In a traceable part of 1 of these giant formations the primary cell was binucleate and harboured 42 mononucleate secondary cells. In 2 cases a secondary cell within 1 of the large primary cells showed a tertiary cell with 1 nucleus (Fig. 4C). One xenoma showed a striking protuberance, apparently made by a parasitic stage directed towards the lumen of the capillary (Fig. 4D). Remainders of xenomas left by the parasitic stages or destroyed xenomas were not found.

DISCUSSION

Paramyxean as well as Myxozoan developmental stages can be found within host cells (Lom, Dykova & Feist, 1989; Ginsburger-Vogel & Desportes, 1979*a*).

All known Paramyxea parasitize marine invertebrate animals (Desportes & Perkins, 1990). Intracellular parasitism is only known from the paramyxean *Paramarteilia orchestiae* (Ginsburger-Vogel & Desportes, 1979*a*). The only representative of this genus shows stages constructed of a primary cell containing 1–12 secondary cells; each of them can hold tertiary and quaternary cells.

Myxozoa occur in invertebrate and vertebrate animals and in contrast to Paramyxea they are not restricted to marine habitats (Lom, 1990; Barnard & Upton, 1994). Different intracellular stages have been reported from various myxozoan species. Some reports deal with intracellular parasitism of epithelial cells of renal tubules. Joseph (1907) described stages of *Chloromyxum protei* parasitizing the kidneys of *Proteus anguinus*. This myxozoan causes the formation of xenomas containing different early myxozoan stages, each of them with more than 1 nucleus, and a hypertrophied deformed host cell nucleus. *Sphaerospora renicola* shows an intracellular extrasporogonic sequence of development in epithelial cells of the kidney tubules from *Cyprinus carpio* (Dykova & Lom, 1982, 1988; Lom & Dykova, 1985). Infected cells fuse to form large syncytia filled with numerous parasitic stages consisting of up to 4 cell generations, one inserted inside the other, and hypertrophic host cell nuclei. The same stages found in carp kidneys were attributed to *Hoferellus cyprini* by other authors (Molnar & Kovacs-Gayer, 1986; Kovacs-Gayer *et al*. 1987; Molnar, 1994). Early intracellular developmental stages of myxozoans also occur, for example in epithelial cells of the intestinal wall of *Branchiura sowerbyi* (Lom *et al*. 1997). Even spore formation can take place intracellularly. For instance *Myxobolus cyprini* produces spores within muscle fibres of *C. carpio* (Molnar & Kovacs-Gayer, 1985). Very large xenomas result from infection of capillary endothelial cells in the kidneys of *Esox lucius* by *Myxidium lieberkuehni* (Lom *et al*. 1989). They contain parasitic stages of up to 3 cell generations and frequently the host cell nucleus is fragmented. In 1993 Baska described intracellular stages of 2 myxozoan species found in *Acipenser ruthenus*. Developmental stages of *Chloromyxum inexpectatum* form xenomas in the capillary network of Bowman's capsules and stages of *Sphaerospora colomani* cause enlargement of endothelial cells of intertubular kidney capillaries.

The xenomas found in kidneys of *E. lucius* and *A. ruthenus* as well as in brains of *Talpa europaea* are similar in the way that the host cells are components of blood capillaries. Some intracellular stages like the early binucleate stages of *C. protei* and the primary cells of *S. renicola* and *M. lieberkuehni* containing 1 secondary cell, look similar to the youngest stages found in *T. europaea* but the subsequent development seems different when taking into account the numbers of cells, cell nuclei and cell generations.

Neither Myxozoa nor Paramyxea developing in homoiothermic vertebrates have been reported to date. The finding of myxozoan spores in stool samples from humans showing gastrointestinal symptoms did not derive from myxozoan infections of these patients. In some cases they evidently were present in fish consumed by the patients (McClelland, Murphy & Cone, 1997; Boreham *et al*. 1998).

There are 2 morphological criteria for identifying the host cells as pericytes: first, there is close contact between xenomas and capillaries, and secondly, the basal lamina surrounds the parasitized cells (Krstic, 1978).

An exact identification of the parasite infecting the brain of moles was impossible because the source of infection and the spores, which are necessary for diagnosis, could not be detected. The stages con-

sisting of parasitic cells inside other cells of the same organism point to a relationship to Myxozoa or Paramyxea. A relationship to Paramyxea seems to be unlikely because of 3 aspects: first, there was no evidence of quaternary cells and of haplosporosomes characteristic for the primary cells of the only known intracellularly parasitizing paramyxean; secondly, the host is a vertebrate; and thirdly, the locality of origin is far away from any marine habitat.

The intracellular stages found in *T. europaea* are quite similar to corresponding stages known from some myxozoans. However, the host is a mammal which is, as far as we know, very unusual for Myxozoa. Two facts support to some extent the possibility for an aberrant infection: all over the year the xenomas contained the same developmental stages, and no other stages of the parasite could be found in organs other than the brain of the host. The first fact mentioned is in contrast to regular seasonal occurrence of developmental stages known for example from *Henneguya doori* parasitizing *Perca flavescens* (Cone, 1994). On the other hand, the infection rate in the moles examined, 30 out of 55, gives good evidence of a possible established (non-accidental) occurrence. Considering these facts, we suggest that the parasitic cells causing the xenomas of moles are classified as myxozoan-like organisms until an exact identification is possible.

Description of the myxozoan-like organism:
Host: *Talpa europaea* L., 1758
Locality: surroundings of Graz, Styria, Austria
Site of infection: pericytes of brain capillaries
Developmental stages: mono- or binucleated primary cells containing 1, 2, 4 or a not precisely definable higher number of secondary cells; in giant stages sometimes tertiary cells;
Deposition of slides: Biologie-Zentrum des Oberösterreichischen Landesmuseums, Linz, Österreich, Europa; Inventory numbers: 1999/120–1999/123; Natural History Museum, Department of Invertebrates, Berne, Switzerland, Europe. Inventory numbers: My1–My4;

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