

A New Species of *Nosema* from *Hylobittacus apicalis* (Insecta: Mecoptera: Bittacidae)

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An undescribed *Nosema* was found infecting adults of the mecopteran *Hylobittacus apicalis*. This microsporidium is described herein as the first record of a microsporidium from the order Mecoptera. The slightly pyriform spores measured $4.5 \times 2.4 \mu\text{m}$. Mature spores had 9.5–10 polar filament coils irregularly grouped in the posterior end. The life cycle and ultrastructure of the developmental stages were described, and were typical of other *Nosema* spp. This microsporidium was regularly recorded from adult *Hylobittacus apicalis* populations over a 10-year period and the incidence of infection increased during the summer.

KEY WORDS: *Nosema apicalis*; *Hylobittacus apicalis*; *Bittacus strigosus*; *Panorpa helena*; Microsporidia; ultrastructure; infection rates.

INTRODUCTION

The Mecoptera represents one of the few orders of insects from which microsporidian parasites have not been reported (Sprague, 1977). During a biological study of Mecoptera, a microsporidium was found infecting the hangingfly *Hylobittacus apicalis*, one of the most common hangingflies in Illinois (Webb et al., 1975). This insect is widely distributed throughout the southern two-thirds of the state. Adults are predaceous on other flying insects, primarily Diptera, and are most commonly collected on jewelweed and stinging wood nettle in moist, shaded, bottomlands. In Illinois, adults are present from the end of April until the beginning of August.

The microsporidium from *H. apicalis* is described in this paper as a new species of *Nosema*.

METHODS

Collection of *H. apicalis* adults. During 1972, adult mecopterans were collected from the Illinois counties shown in Figure 1. From 1971 through 1976, adults were collected on the dates shown in Table 1, from an area adjacent to the Illinois River in Marshall County, Illinois. During 1981,

adult mecopterans were collected each week from April to September at the same Marshall County area. All specimens were collected with an insect net as they hung from low vegetation or while they were in flight.

Light microscope observations. Mecoptera collections were refrigerated in a portable cooler until returned to the laboratory for examination. Collections not examined immediately were frozen until they could be examined. Infections were diagnosed by the presence of spores in wet-mount preparations of fat body and midgut epithelium. Developmental stages were prepared by smearing infected tissue on a cover glass, drying for 30 min, fixing in absolute methanol for 10 min, and staining in a 10% aqueous solution of Giemsa for 30 min. The tissues infected by this microsporidium were determined by sectioning infected adults using the method described by Brooks (1970). Fresh spores were immobilized with dilute agar by the method of Vavra and Maddox (1976) and measured under an oil immersion objective with a Cooke image-splitting eyepiece.

Electron microscope observations. Infected tissues were fixed overnight in 5% gluteraldehyde buffered with 0.1 M caco-

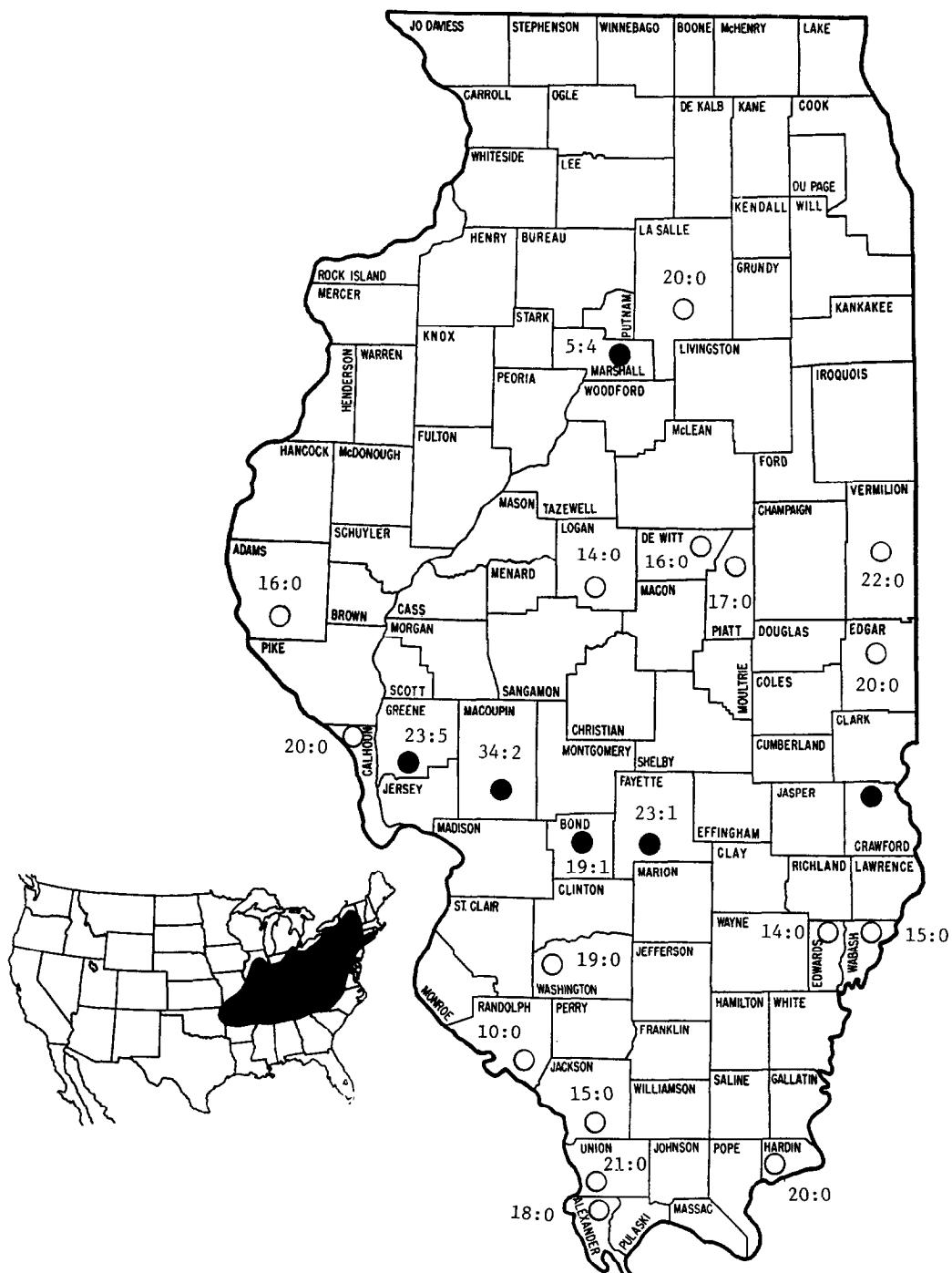


FIG. 1. Collection localities of *Hylobittacus apicalis* (●, infected; ○, not infected) in Illinois during 1972. The ratio given at each locality indicates the number of specimens examined compared to the number of specimens infected. The insert map shows the distribution of *H. apicalis* in North America.

TABLE I
INCIDENCE OF *NOSEMA APICALIS* INFECTIONS IN
HYLOBITTACUS APICALIS ADULTS COLLECTED 7
MILES SOUTH OF LACON, MARSHALL COUNTY,
ILLINOIS

| Date collected | <i>Hylobittacus apicalis</i> | |
|----------------|------------------------------|---------------|
| | No. examined | % Infected |
| 1971 | | |
| July 8 | 9 | 77.8 |
| July 19 | 23 | 78.3 |
| 1972 | | |
| Aug. 1 | 1 | 100 |
| 1973 | | |
| July 19 | 20 | 80.0 |
| 1974 | | |
| June 26 | 26 | 20.0 |
| 1975 | | |
| June 15 | 49 | 10.2 |
| June 30 | 6 | 100 |
| 1976 | | |
| July 16 | 29 | 68.0 |

dylate to pH 7.5. After gluteraldehyde fixation, tissues were washed in buffer for 30 min, post-fixed in 1% osmium tetroxide for 2 hr, dehydrated in ethanol, and embedded in low-viscosity resin (Spurr, 1969). Tissue was sectioned with a diamond knife and stained with 5% uranyl acetate followed by lead citrate (Reynolds, 1963). Sections were examined and photographed with a Zeiss 9-S electron microscope.

Cross transmission studies. Cross transmission studies were conducted on three species of lepidopterous larvae using the method of Nordin and Maddox (1974). Because laboratory cultures of Mecoptera were not available and are very difficult to maintain, cross transmission studies were not conducted on other species of Mecoptera.

RESULTS

Light Microscope Observations

Midgut epithelium and fat body were the primary sites of infection. The infection developed first in the midgut then the fat body. In heavily infected individuals most

of the fat body cells were infected. Infections were not detected in the ovaries of infected females or in eggs laid by infected females.

Schizonts in Giemsa-stained smears were typically binucleate or tetranucleate (Fig. 2A, B), with the schizogonic sequence presumably being binary fission of tetranucleate schizonts. Developmental forms resembling uninucleate schizonts were occasionally observed (Fig. 2C). Uninucleate forms always had nuclei with irregular shapes making conformation of the uninucleate condition difficult.

Sporogony was characteristic of the genus *Nosema* as described by Sprague (1978). Diplocaryotic sporonts (Fig. 2D) underwent nuclear division (Fig. 2E, F) followed by binary fission to form binucleated sporoblasts and finally spores (Fig. 2G). Fresh spores (Fig. 3) were slightly pyriform in shape and measured $4.5 \pm 0.6 \times 2.4 \pm 0.2 \mu\text{m}$ (range $4.1-5.2 \times 2.1-2.9 \mu\text{m}$).

Electron Microscope Observations

In sporonts (Fig. 4A) the nuclei are surrounded by a double membrane; rough endoplasmic reticulum and free ribosomes are present in the cytoplasm and the cell is enclosed in a single unit membrane.

The progressive features of spore morphogenesis are illustrated in Figures 4A-D. The early sporoblast (Fig. 4B) is easily differentiated from schizonts by the thicker cell membrane, more extensive rough endoplasmic reticulum and the well-developed Golgi apparatus. A later sporoblast (Fig. 4C) has a thicker cell membrane and evidence of polar filament formation, while the most advanced sporoblast (Fig. 4D) has become more condensed than earlier forms, has several well-developed polar filament coils and a multilayered spore coat. All developmental forms involved in spore morphogenesis were binucleate.

Spores (Fig. 5A, B) were binucleate with a large posterior vacuole, bounded by a distinct membrane. Probably, as a result of this large posterior vacuole, most spores

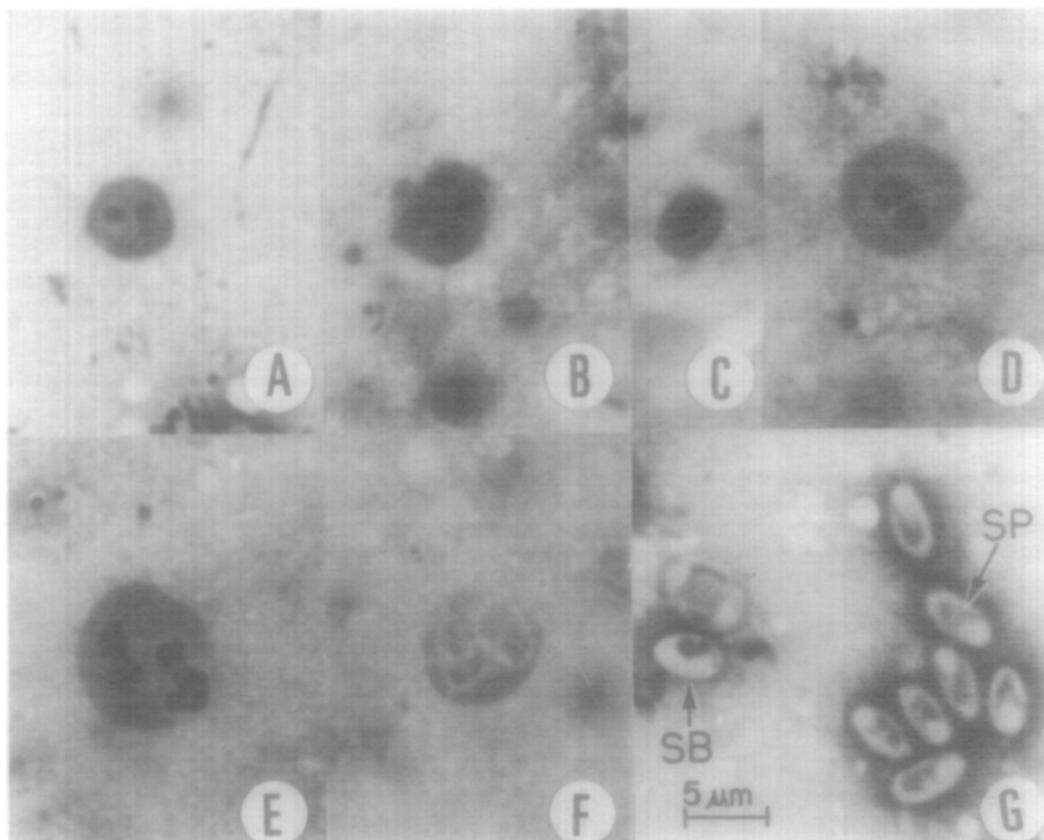


FIG. 2. Giemsa-stained developmental stages of *N. apicalis*. (A) Binucleate schizont. (B) Tetranucleate schizont. (C) Mononucleate schizont. (D) Sporont with nuclei in diplokaryon arrangement. (E) and (F) Dividing sporont. (G) Late sporoblast (SB) and spores (Sp).

prepared for electron microscopy had an invaginated posterior end (Fig. 5A). Over 90% of the mature spores in electron microscope preparations from 20 host specimens had invaginated posterior ends. This was undoubtedly a fixation artifact as this invaginated condition was not observed in preparations of fresh spores or Giemsa-stained spores. Mature spores had from 9.5 to 10 polar filament coils irregularly grouped in the posterior end of the spore. Coils averaged 116 nm in diameter and were never arranged in a single file laterally. Rough endoplasmic reticulum densely populated with ribosomes was layered in cytoplasmic areas of the spore. The spore envelope had three layers as identified by Vavra (1976): an outer electron-dense layer,

the exospore; a middle electron-transparent area, the endospore; and an inner unit membrane. The exospore layer averaged 20 nm in thickness and was of a uniform thickness around the entire spore. The endospore layer was 100 nm thick around all portions of the spore except in the area over the polar cap, where it was only 18 nm thick. The polaroplast consisted of two distinct regions, an anterior region of tightly packed lamellae and a more vesicular posterior region (Fig. 6). The lamellae in the anterior region were 10 nm thick and were constructed of three membranes (Fig. 7). The anchoring disk of the polar filament, located in the anterior portion of the spore (Fig. 6), extended posteriorly along the inner spore membrane. The manubroid por-

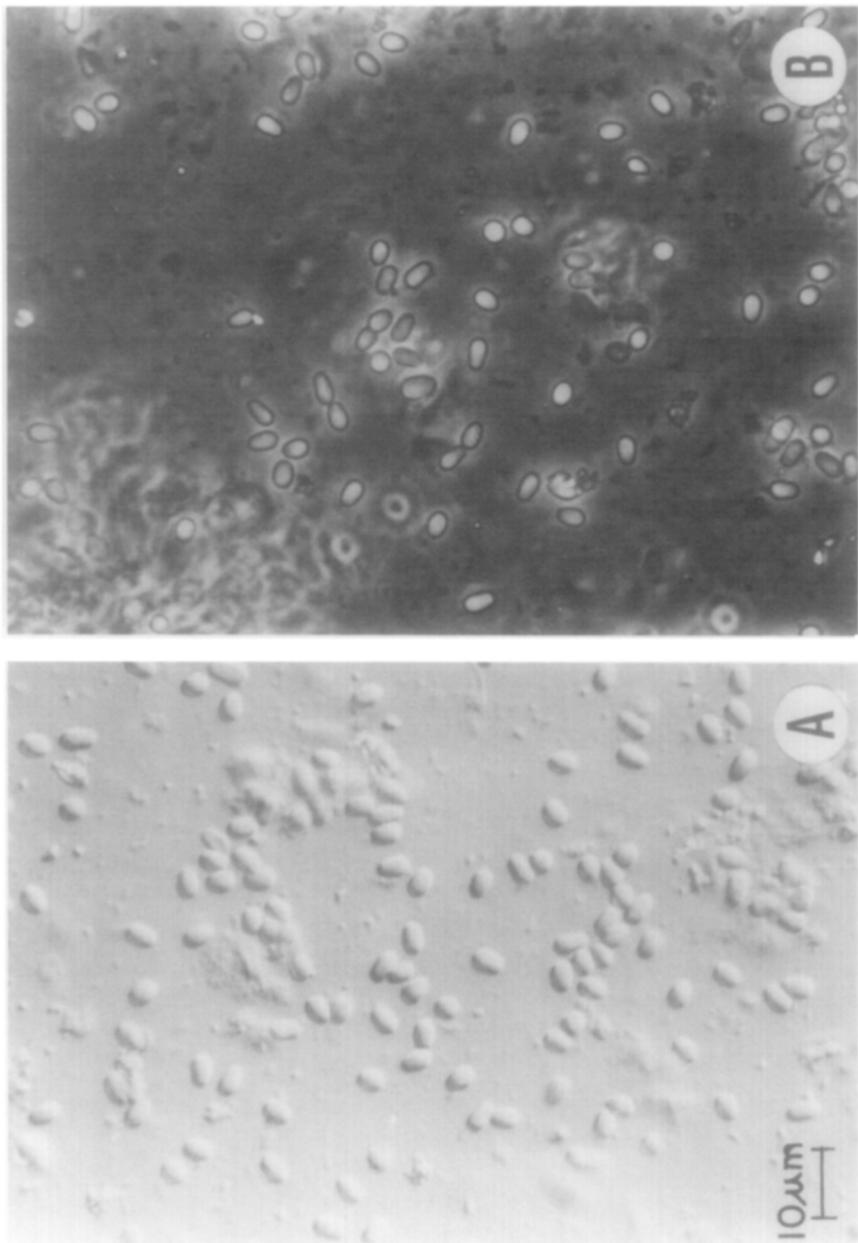
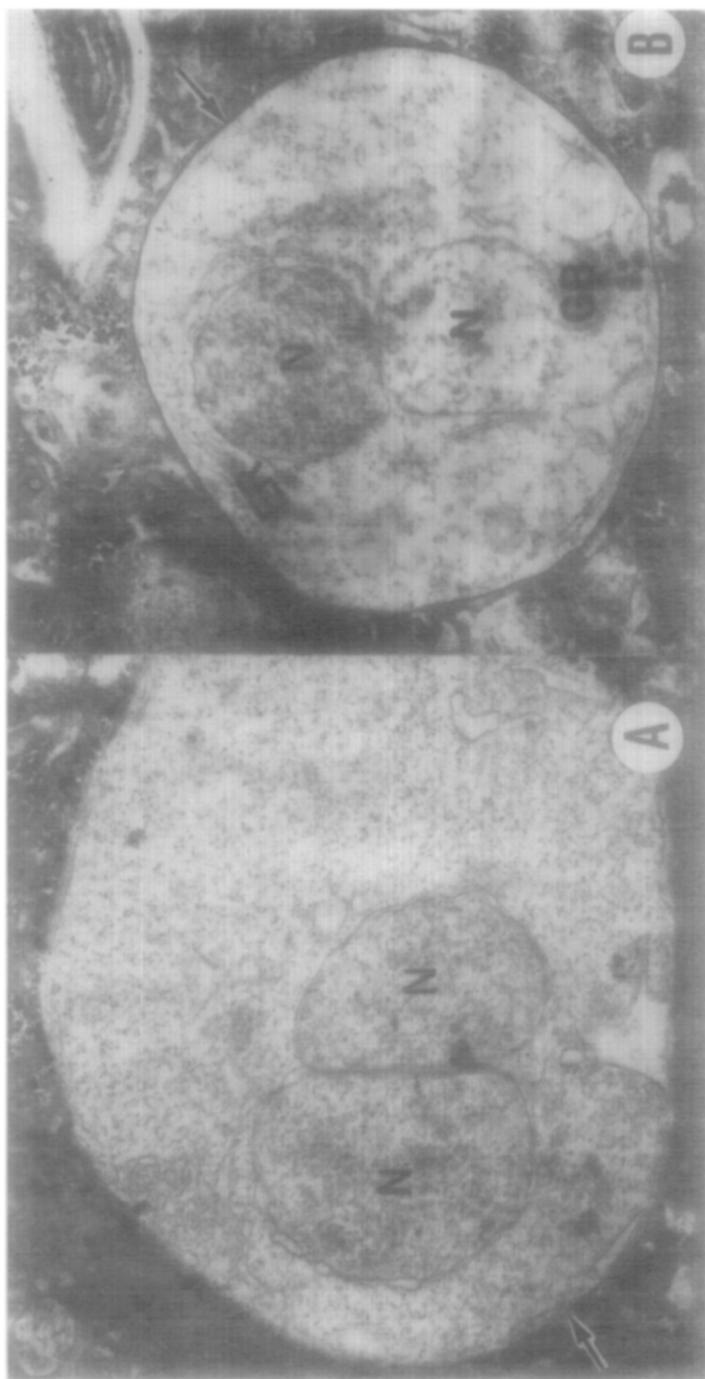


FIG. 3. Fresh, unfixed spores of *N. apicalis* in squash preparation from infected adult fat body. (A) Nomarski interference contrast. (B) Phase contrast.



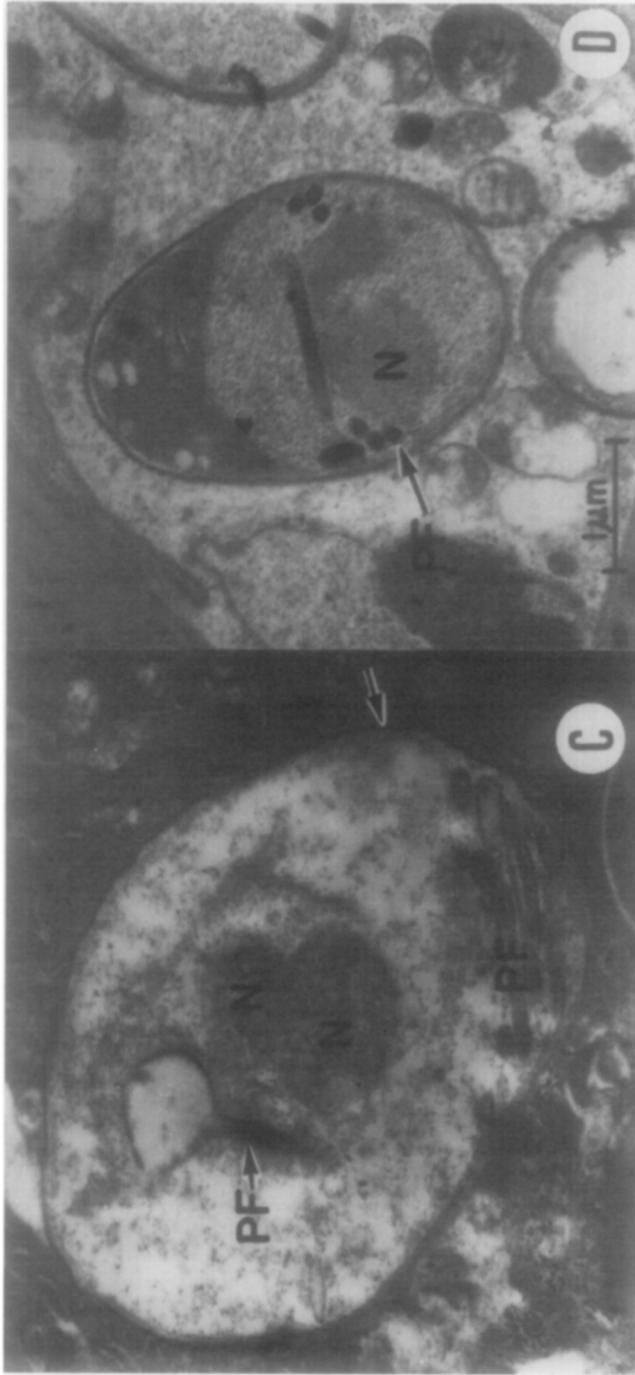


FIG. 4. electron photomicrograph sporogonic stages of *N. apicalis*. (A) Sporont with nuclei (N) in diplokaryon arrangement, note thin plasma membrane. (B) An early sporoblast characterized by a more well developed Golgi body (GB) and a thickening of the plasma membrane. (C) Later sporoblast showing additional thickening of plasma membrane and the beginning of polar filament (PF) formation. (D) A very late sporoblast with layers of spore coat beginning to form, polar filament has begun arrangement as in the mature spore, and cytoplasm has become more electron dense.

tion of the polar filament enlarged to a diameter of 190 nm at its attachment to the anchoring disk.

Host Range Studies

Nosema apicalis spores fed to neonate larvae of the three lepidopteran species, *Diacrisia virginica*, *Pseudaletia unipuncta*, and *Spodoptera exigua* produced no infections.

Incidence of Nosema apicalis in Mecopteran Populations

Field collected adults of three mecopteran species, *Hylobittacus apicalis*, *Bittacus strigosus*, and *Panorpa helena* were infected with *N. apicalis*, but infection rates were very low in both *B. strigosus* and *P. helena*. Less than 0.5% of all *P. helena* adults were infected and infections were only found in 1981 collections from one site in Illinois. Only 2.9% of the *B. strigosus* adults were infected, although infected *B. strigosus* adults were recovered from several different collection sites during 1973, 1974, 1975, and 1981. Table 1 summarizes the incidence of infection in *H. apicalis* adults collected from the study area in Marshall County, Illinois, during the years 1971–1976. The geographical distribution of *H. apicalis* in North America, the location of *H. apicalis* collection sites in Illinois, and the incidence of *N. apicalis* in these collections are given in Figure 1.

The 1981 seasonal incidence of infection in *H. apicalis* adults collected at weekly intervals from the Marshall County study area is given in Table 2. The number of individuals captured on a particular date is not a totally accurate estimate of *H. apicalis* population density because the time spent collecting was not standard for each date. The number collected is, however, a good indicator of the period of time *H. apicalis* adults were present at the collection site and when peak populations occurred. The infection rate tended to increase throughout the season and was almost three times higher in females than in males.

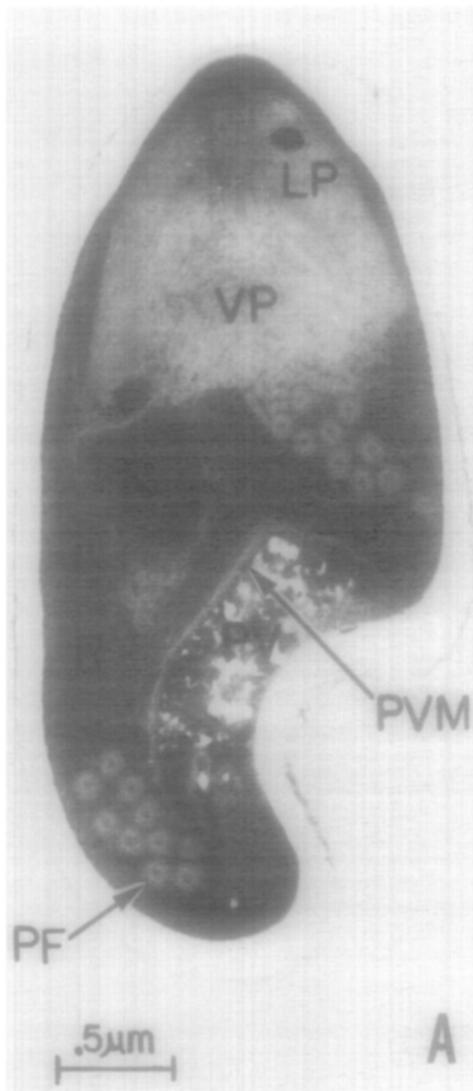


FIG. 5. Longitudinally sectioned spores of *N. apicalis*. (A) Spore with lamellar (LP) and vesicular (VP) regions of the polaroplast, endoplasmic reticulum (heavily populated with ribosomes), posterior vacuole (PV) (bounded by a membrane), and 9.5 polar filament coils (PF). This plane of sectioning is at such an angle that only one nucleus is visible. This spore possesses the invaginated posterior end characteristic of most spores fixed for TEM. (B) In addition to the features seen in A, this section demonstrates the presence of two nuclei, the exospore (EX), endospore (EN), and cytoplasmic membrane (CM). The rare uninvoluted condition is also evident in this section.

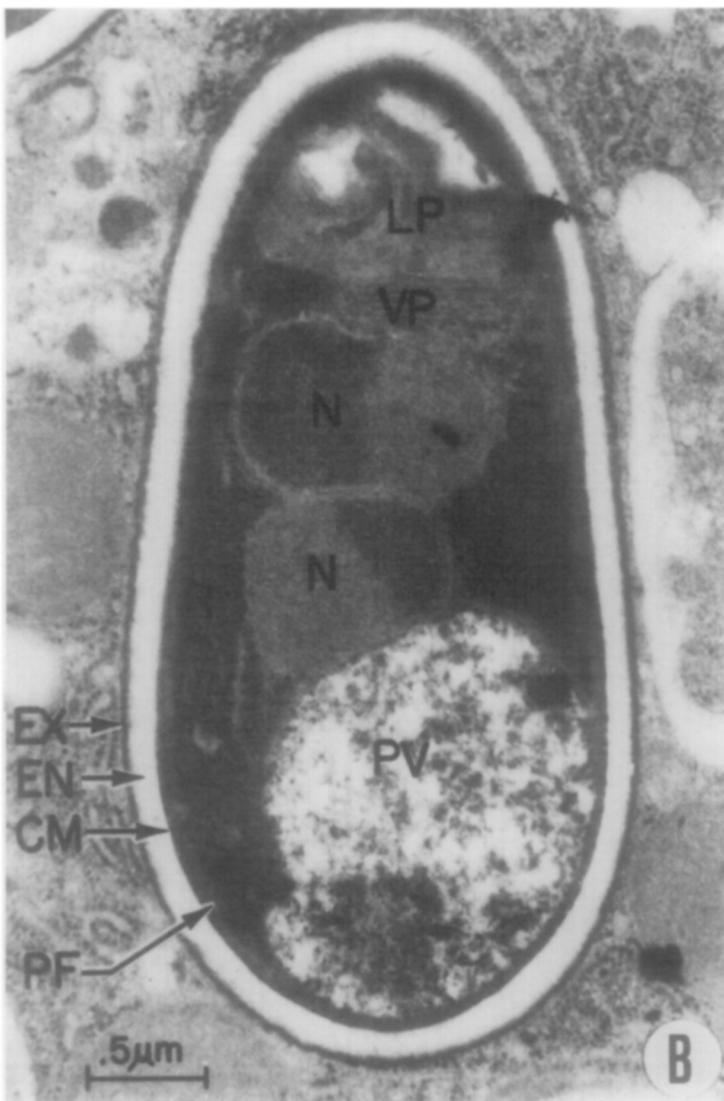


FIG. 5—Continued.

DISCUSSION

Nosema apicalis is the first microsporidium reported from the insect order Mecoptera, but species of the mecopteran family Bittacidae are predators of small arthropods, primarily adult dipterans (Setty, 1940). This creates the possibility that *N. apicalis* is a microsporidium indigenous to adult dipterans but infectious to predatory *H. apicalis* adults.

Eight species of *Nosema* have been described from species of Diptera (Table 3).

No ultrastructural information is available for *Nosema bibionis*, *N. binucleatum*, *N. cheisini*, *N. chironomi*, *N. sphaeromiadis*, or *N. strictum*, and with the exception of the Brazilian species, *N. chironomi*, all preceding species were described from European hosts. The meager information available in the descriptions of these species makes comparison with *N. apicalis* difficult. However, since these microsporidia have never been reported from North America, have slightly different spore sizes, infect different host tissues, or have

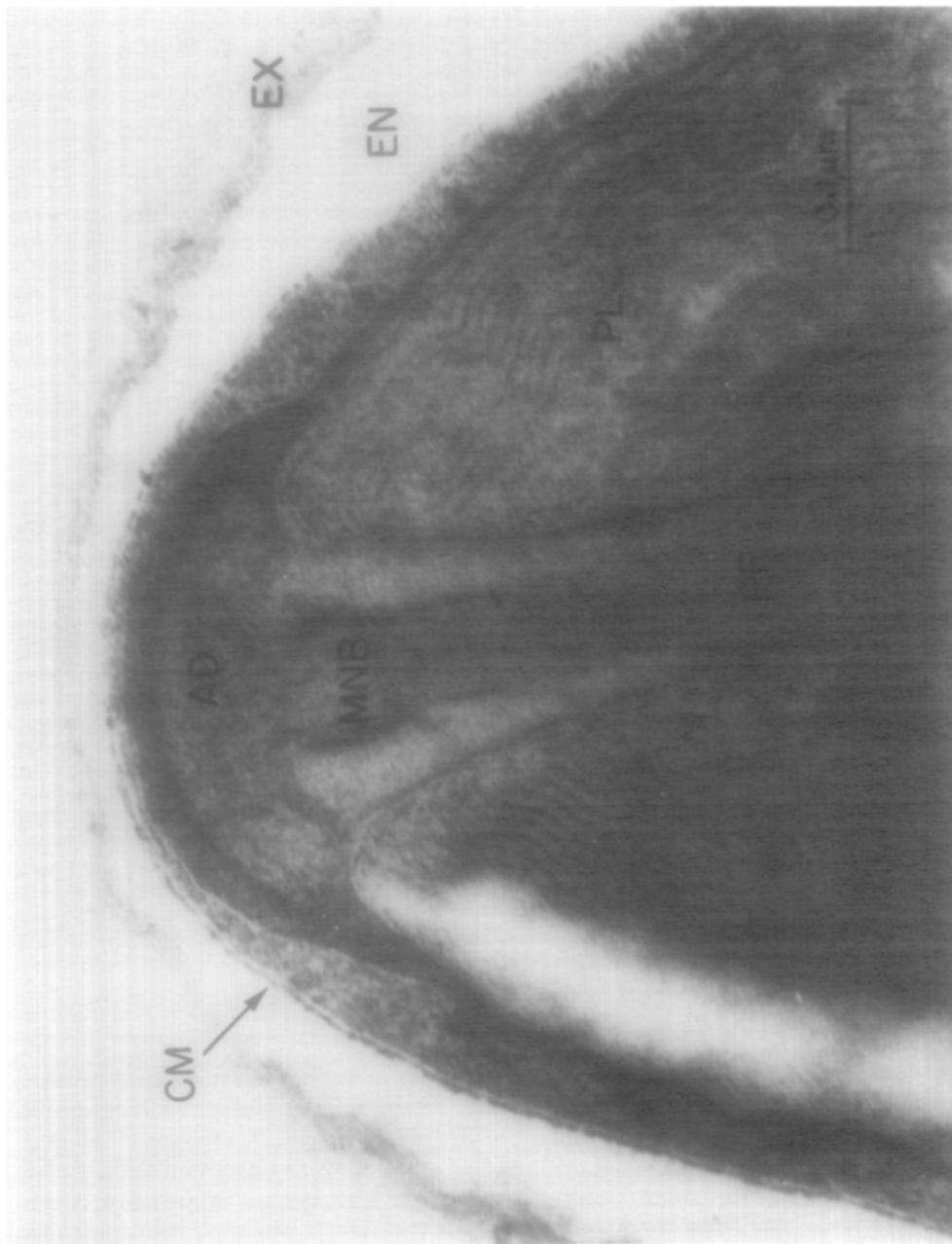


FIG. 6. Longitudinal section through anterior end of *N. apicalis* spore demonstrating the three layers of the spore coat; exospore (EX), endospore (EN), and cytoplasmic membrane (CM); the anchoring disk and manubroid (MNB) parts of the polar filament (PF); and the lamellar polaroplast (PL).

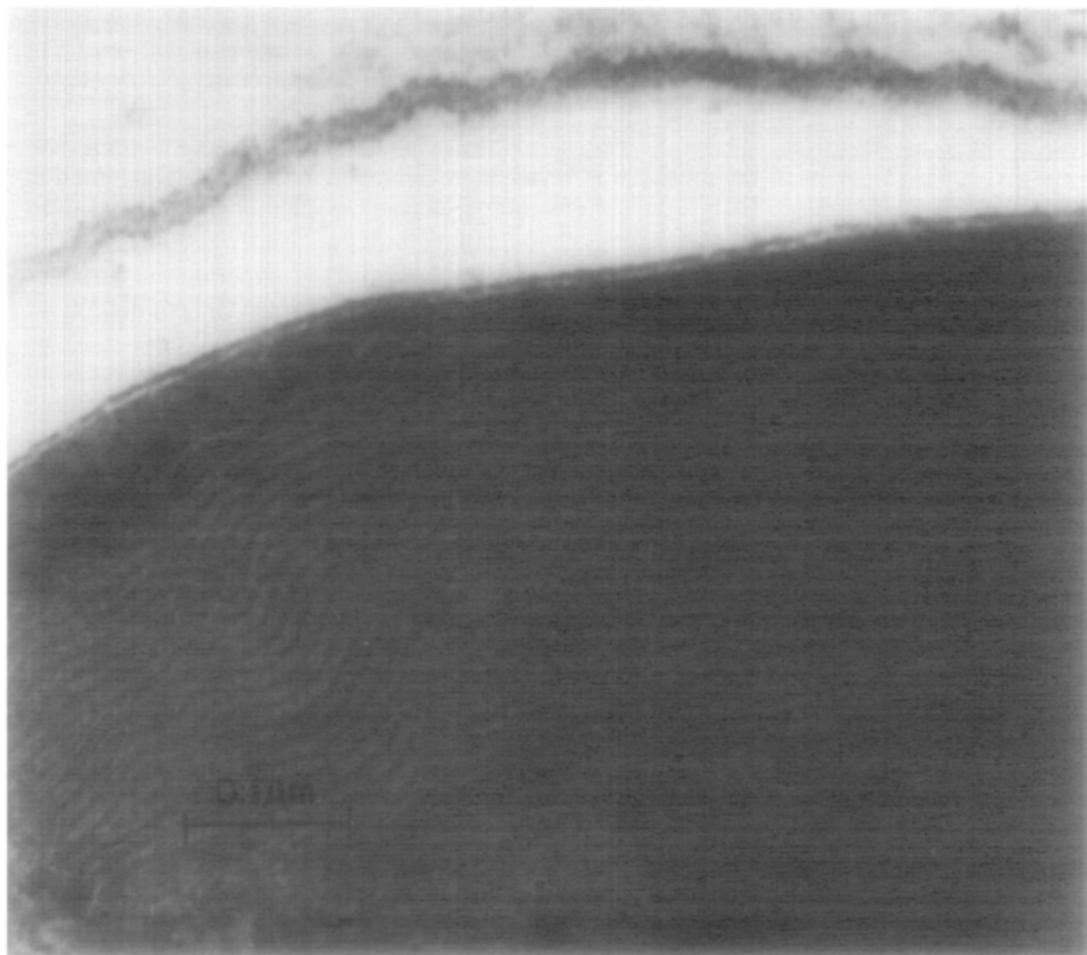


FIG. 7. The lamellar region of the polaroplast of an *N. apicalis* spore. Each lamellae is constructed of three membranes.

different developmental forms, it is highly unlikely that any of these species are conspecific with *N. apicalis*.

Nosema algerae was described from a laboratory colony of *Anopheles stephensi* in Illinois, but probably originated from Africa or Asia (Vavra and Undeen, 1970). *N. algerae* was infectious to neonate lepidopteran larvae while *N. apicalis* was not. The ultrastructural features of *N. algerae* spores (Canning and Sinden, 1973) included no prominent posterior vacuole and the coils of the polar filament were arranged in a straight line. *N. apicalis* had a prominent posterior vacuole and the polar filament coils were not in a straight line.

N. kingii was described from a laboratory

colony of *Drosophila willistoni* (Kramer, 1964). The polar filament coils of *N. kingii* were arranged in a straight line (Burnett and King, 1962), unlike the arrangement of coils in *N. apicalis*. *N. kingii* spores from a paratype slide were uniformly oval while *N. apicalis* were slightly pyriform.

The widespread distribution of *N. apicalis* in Illinois populations of *H. apicalis* and the recurring infections in populations of this mecopteran over a 10-year period (Tables 1, 2) provide additional evidence that *N. apicalis* is a primary pathogen of *H. apicalis*.

We could not maintain a laboratory colony of any mecopteran species and were, therefore, unable to determine if *N. api-*

TABLE 2
SEASONAL INCIDENCE OF *NOSEMA APICALIS* INFECTIONS IN *HYLOBITTACUS APICALIS* ADULTS COLLECTED 7 MILES SOUTH OF LACON, MARSHALL COUNTY, ILLINOIS, DURING 1981

| Date | Male | | | Female | | | 'Total male + female collected' | % Infected | 'Total male + female infected' | % Infected |
|-----------|--------------------|-----------------|---------------|--------------------|-----------------|---------------|------------------------------------|------------|-----------------------------------|------------|
| | Total collected | No. examined | % Infected | Total collected | No. examined | % Infected | | | | |
| April 14 | 0 | 0 | — | 0 | 0 | — | — | — | 0 | — |
| June 2 | 0 | 0 | — | 0 | 0 | — | — | — | 0 | — |
| June 15 | 11 | 10 | 0 | 16 | 10 | 10.0 | 27 | 5.0 | — | — |
| June 29 | 14 | 10 | 0 | 20 | 10 | 0 | 34 | 0 | — | — |
| July 2 | 10 | 10 | 0 | 30 | 14 | 14.2 | 40 | 8.3 | — | — |
| July 10 | 8 | 8 | 50.0 | 12 | 12 | 91.7 | 20 | 75.0 | — | — |
| July 17 | 3 | 3 | 66.7 | 7 | 6 | 85.7 | 10 | 88.9 | — | — |
| July 24 | 1 | 1 | 0 | 3 | 3 | 66.7 | 4 | 50.0 | — | — |
| August 4 | 0 | 0 | — | 1 | 1 | 100.0 | 1 | 100.0 | — | — |
| August 16 | 0 | 0 | — | 0 | 0 | — | 0 | — | 0 | — |
| Total | 47 | 42 | 14.3 | 89 | 56 | 41.1 | 136 | 29.6 | — | — |

calis infects larval mecopterans or how the predatory adults acquire infections from other infected mecopterans. Setty (1940) reported that *H. apicalis* adults are cannibalistic in cages but it is not known if cannibalism occurred in the field. The infection rate increased throughout the summer until the adults could no longer be collected (Tables 1, 2). Thus, the infection must spread horizontally throughout the population or *H. apicalis* adults must have an increasing source of infected prey. The adult females have an infection rate about three times that of males. This could be the result of a behavioral difference influencing horizontal transmission, or the larger females could consume greater numbers of infected prey. Since many of the *H. apicalis* adults were heavily infected with *N. apicalis*, this microsporidium is probably an important mortality factor in *H. apicalis* populations.

An obvious void in our information on the biology of *N. apicalis* is what effect, if any, this microsporidium has on *H. apicalis* larvae. Since the infection is not transovarially transmitted, it is possible that *N. apicalis* only infects adult Mecoptera.

SYSTEMATICS

Nosema apicalis n. sp.

Host species. Primary host: *Hylobittacus apicalis* (Insecta: Mecoptera: Bittacidae) adults. Occasional hosts: *Bittacus strigosus* (Insecta Mecoptera: Bittacidae) adults and *Panorpa helena* (Insecta: Mecoptera: Panorpidae) adults.

Host tissues infected. Midgut, fat body.

Type locality. Marshall County, Illinois; 7 miles south of Lacon.

Deposition of types. Slide with holotype in the International Protozoan Type Slide Collection, Smithsonian Institution, Washington, D. C., Paratypes in the collections of E. Hazard, Lake Charles, Louisiana; J. Weiser, Prague, Czechoslovakia; and in the collection of the senior author, J. V. Maddox, Illinois Natural History Survey, Champaign, Illinois.

Schizionic stages. Schizonts typically

TABLE 3
CHARACTERISTICS OF *Nosema* SPECIES DESCRIBED FROM DIPTERAN HOSTS

| Species | Host(s) | Spore size (μm) | Tissue(s) infected | Location | Reference |
|--------------------------|--|------------------------------|----------------------------|-------------------------------------|-----------------------------|
| <i>N. algerae</i> | <i>Anopheles stephensi</i> Adults and larvae | 4.3 × 2.6 | Most tissues | Laboratory Colony, United States | Vávra and Undeen, 1970 |
| | Many other species experimentally | 3.5–5 × 2.5–4 | Muscle | Germany | Stammer, 1956 |
| <i>N. bibionis</i> | <i>Bibio varipes</i> larvae | 4.4–6.8 × 2.6–2.8 | Midge | Switzerland, Czechoslovakia | Weissenberg, 1926 |
| <i>N. binucleatum</i> | <i>Tipula sigenita</i> larvae | 8.5–9 × 4 | Fat Body | Czechoslovakia | Weiser, 1963 |
| <i>N. cheistini</i> | <i>Prodiamesa olivacea</i> | 2–3 × 1.5–2 | Epithelium of hindgut | Brazil | Lutz and Splendore, 1968 |
| <i>N. chironomi</i> | <i>Ablabesmyia lentiginosa</i> | 4.3 × 2.6 | Fat body, gonads midgut | Laboratory Colony, United States | Kramer, 1964 |
| <i>N. kingii</i> | <i>Chironomus</i> sp. <i>Drosophila willistoni</i> Adults, plus many other Diptera experimentally | 5.6 × 2.5 | Fat body | Czechoslovakia | Weiser, 1961 |
| | <i>Sphaeromias</i> sp. | 5 × 1.5 | No data | France | Moniez, 1887 |
| <i>N. sphaeronioidis</i> | <i>Pachyphasma pratensis</i> | 3–4 × 2–2.5 | Midgut | Czechoslovakia | Weiser, 1946 |
| <i>N. strictum</i> | <i>Chironomus thummi</i> | | | | |
| <i>N. zavreli</i> | larvae | | | | |

binucleate or tetranucleate with schizonic sequence by binary fission of tetranucleate schizonts.

Sporogonal stages. Sporont with nuclei in diplokaryon arrangement gives rise to two spores, each having nuclei in diplokaryon form.

Spore. Slightly pyriform in shape. Average spore measurements $4.5 \pm 0.6 \times 2.4 \pm 0.2 \mu\text{m}$. Spore surface without appendages. Mature spores have 9.5–10 polar filament coils irregularly grouped in posterior end of spore. Coils averaged 116 nm in diameter. Large posterior vacuole with distinct membrane. Posterior end of spore usually invaginated after EM preparation. Polaroplast with two regions, an anterior lamellar region and a posterior vesicular region. Nuclei in diplokaryon arrangement.

Derivation of name. *apicalis* after specific name of primary host *H. apicalis*.

Differentiating characters. The combination of spore size and shape, arrangement of polar filament, and presence of a large posterior vacuole distinguish this species from other *Nosema* sp. for which ultrastructural information is available. In addition, other data presented in this paper suggest that *N. apicalis* is exclusively a parasite of Mecoptera and there are no previous reports of microsporidia from representatives of the order Mecoptera.

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