Classification of the Haplosporidia

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Introduction

The name "haplosporidia" is a vernacular term, derived from the familiar ordinal name HAPLOSPORIDIA Caullery & Mesnil, 1899, spelled HAPLOSPORIDA since 1964 when the Honigberg Committee adopted uniform endings for ordinal names. The vernacular term is used at this time with reference both to organisms in the order HAPLOSPORIDA and to others that seem to be closely related to them. It is a useful term now, while we are developing a classification and searching for names of new taxa. However, I hasten to emphasize the fact that the haplosporidia are not simple and to urge that in the future, we try to limit the use of names (vernacular and technical) that suggest simplicity.

Caullery and Mesnil (1899a, b) established the genus *Aplosporidium* for two new species, *A. scolopli* and *A. heterocirri,* found in marine annelids. They grouped this genus with *Bertramia* C. and M., 1897, *Coelosporidium* Mesnil and Marchoux, 1897, and an unnamed parasite reported by Schewiakoff (1893). For this group they established a new order, called it "APLOSPORIDIES," and placed it in the class SPOROZOA Leuckart, 1879. The order was said to be characterized by a simplicity of life cycle and of spore structure. The "simplicity" of the spores had special reference to the lack of a polar capsule and/or polar filament as seen in the CNIDOSPORIDIA Doflein, 1901.

Caullery and Mesnil (1899b) gave the order the Greek root for "simple" and specifically stated that they based the name APLOSPORIDIES on it because of the simplicity of the organisms. Lühe (1900) stated however, that the spelling they used, "Aplo-," is correct transliteration of another Greek root (with the same spelling but different accent marks) that means "non-navigable." Therefore, he emended the names to *Haplosporidium* and HAPLOSPORIDIA so they would contain the intended meaning, "simple." Since then there has been some confusion about whether the emended names should be attributed to Caullery and Mesnil or to Lühe. Lühe (1900) himself, attributed them to Caullery and Mesnil. Kudo (1931), in the first edition of his protozoology text, used, without stating reasons, HAPLOSPORIDIA Lühe and *Haplosporidium* Caullery and Mesnil. In later editions he attributed (again without giving reasons) both names to the latter authors. I have argued (Sprague, 1963) that *Aplosporidium* is an incorrect transliteration and, according to Article 32 of the Code (see Stoll, 1961) should be regarded as correct original spelling. In this case, according to Article 33, the emended form *Haplosporidium* would be attributable to Lühe (1900). Although *Aplosporidium* Caullery and Mesnil, 1899, has priority over *Haplosporidium* Lühe, 1900, I held that the former should be regarded as a nomen oblitum (Article 23). Until now I have continued to hold this view (Sprague, 1963, 1966a, 1970) because I felt that strict application of the Code required it. However, I held it reluctantly because of a feeling that credit for establishing the name *Haplosporidium,* regardless of rules of nomenclature, properly belongs to Caullery and Mesnil. Now, I think I see a way of interpreting the Rules that resolves the problem. The Rules provide for emendation of a name if "there is in the original publication clear evidence of an inadvertent error, such as a lapsus calami, or a copyist's or printer's error (incorrect transliterations . . . not to be considered inadvertent error . . .)" (Article 32). Clearly, a name cannot be justifiably emended merely because there was incorrect transliteration. However, in this particular case, we can take the position that the name *Aplosporidium* can be justifiably emended on the grounds that the authors clearly intended to convey one meaning but inadvertently conveyed another. Therefore, I propose that we treat Lühe's change of spelling from *Aplosporidium* to *Haplosporidium* as a correction of an "inadvertent error" and a "justified emendation," in which case the name *Haplosporidium* "takes the date and authorship of the original spelling" (Article 33). Regarding the ordinal name HAPLOSPORIDIA (-IDA), the rules of nomenclature do not apply and common courtesy requires that we attribute this name to Caullery and Mesnil, 1899a.

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Relation of the HAPLOSPORIDIA to the System of the PROTOZOA

Caullery (1953) elevated the haplosporidia to class rank, naming them HAPLOSPOREA and appending them to the SPOROZOA. Most authors, however, treated them as an order in the class SPOROZOA until after the Honigberg (1964) Committee separated this class into subphylum SPOROZOA Leukart, 1900, and subphylum CNIDOSPORA Doflein, 1901. The Committee did not know what to do with the haplosporidia but, "rather leave the HAPLOSPOREA in limbo," put this

class in the subphylum SPOROZOA. Sprague (1965) suggested that class HAPLOSPOREA, having sporoplasms, be removed from the SPOROZOA, which have sporozoites, and placed in the CNIDOSPORA (for which an appropriate new name, PLASMOSPORA, was suggested) with other groups that have sporoplasms. Soon after I suggested (Sprague, 1966b) that haplosporidia are so much like microsporidia that they be reduced to ordinal rank and placed in class MICROSPOREA Corliss and Levine, 1963, with order MICROSPORIDA Balbiani, 1882. The idea that haplosporidia are related to microsporidia was not original with me. It was originated by Caullery and Mesnil (1905). In 1969, being impressed by the ideas of Lom and Vávra (1962), Vávra (1966), and Lom and Corliss (1967) that myxosporidia and microsporidia (which had been lumped together as CNIDOSPORA) are completely unrelated, I proposed (Sprague, 1969) that these two groups be separated and elevated to subphylum rank, becoming subphyla MYXOSPORA and MICROSPORA. These two taxa have been generally accepted and are now used in the systematics part of Zoological Record. Thus, HAPLOSPOREA and MICROSPOREA became recognized as the constituent classes of subphylum MICROSPORA.

During recent years, when several electron microscope studies have given us much greater understanding of both microsporidia and haplosporidia, I have become increasingly impressed by the complexity of haplosporidia and dissatisfied with my expressed view that they and the microsporidia are closely related. This feeling is based mainly on increasing evidence that haplosporidian spores are multicellular structures with peculiar modes of development, whereas the microsporidia clearly have unicellular spores with their own peculiar type of development. As long ago as 1911, Cépède thought that the sporoblast of *Anurosporidium pelseneeri* Caullery and Chappellier, 1906, divides into two cells, one a parietal cell and the other a sporoplasm that becomes enveloped by the parietal cell. Ormières et al. (1973), in an electron microscope study of a new species of *Urosporidium, U. jiroveci,* found inconclusive evidence for the same idea. Now, as a result of recent electron microscope studies by Grizel, Comps, Cousserans, Bonami, and Vago (1974), Grizel, Comps, Bonami, Cousserans, Duthoit, and Le Pennec (1974), Perkins (1976), and Perkins and Wolf (1976), we have conclusive evidence that *Marteilia refringens* and *M. sydneyi* have multicellular spores. Furthermore, envelopment of one cell by another may be a feature common to *Marteilia* and the typical haplosporidia. As a result of the new evidence, I have recently (Sprague, 1977) concluded that microsporidia and haplosporidia are unrelated to one another and should be classified separately. Furthermore, I proposed that each taxon be elevated to phylum rank. This proposal is not as radical as it may seem to some nontaxonomists, for many protozoologists now regard the old phylum PROTOZOA Goldfuss, 1818, as an artificial assemblage of protists, consisting of several unrelated groups. For example, Corliss (1974) has already elevated the ciliates to phylum rank. The Committee on Systematics and Evolution of the Society of Protozoologists, headed by Norman Levine, is now considering my recent proposal.

As I look back over Cépède's (1911) paper for the first time in several years, I am now more impressed than before by the fact that he compared haplosporidia with myxosporidia, which have multicellular spores with parietal cells. Perhaps we have not yet given due consideration to the idea that haplosporidia are related to myxosporidia [which have been shown by Lom (1969) to be definitely related to the coelenterates], but I am not prepared to pursue this idea now.

Internal Classification of the HAPLOSPORIDIA

Several classifications of the haplosporidia have been published. They are reviewed here in chronological order.

Classification by Caullery and Mesnil, 1899b

Class SPOROZOA Leukart, 1879
- Order [H]APLOSPORIDIA C. & M., 1899 (one of several orders).
  - Genus [*H*]*aplosporidium* C. & M., 1899.
  - Genus *Bertramia* C. & M., 1897.
  - Genus *Coelosporidium* Mesnil & Marchoux, 1897.
  - Genus unnamed Schewiakoff.

Classification by Caullery and Mesnil, 1905

Class SPOROZOA L., 1879
- Order HAPLOSPORIDIA C. & M., 1899.
  - Family HAPLOSPORIDIIDAE n. fam.
    - Genus *Haplosporidium* C. & M., 1899.
    - Genus *Urosporidium* C. & M., 1905.
  - Family BERTRAMIIDAE n. fam.
    - Genus *Bertramia* C. & M., 1898.
    - Genus *Ichthyosporidium* C. & M., 1905.
  - Family COELOSPORIDIIDAE n. fam.
    - Genus *Coelosporidium* Mesnil & Marchoux, 1899.
    - Genus *Polycaryum* Stempell, 1901.
    - Genus *Blastulidium* Perez, 1903.
  - Forms of doubtful affinities.
    - Genus *Scheviakovella* n.g.
    - Genus *Chytridiopsis* Schneider, 1884.

It should be noted that Caullery and Mesnil (1905) added to the HAPLOSPORIDIA several genera of protists presumed to have "simple" spores. For a half century thereafter it was customary for protozoologists to put into the HAPLOSPORIDIA organisms that had "simple" spores and did not obviously belong to another group. Thus, this group became what Mackin and Loesch (1954) called "the haplosporidian wastebasket."

Classification by Kudo, 1931

Class SPOROZOA L., 1879
- Order HAPLOSPORIDIA Lühe, 1900.
  - Genus *Haplosporidium* C. & M., 1899.

Genus *Urosporidium* C. & M., 1905.
Genus *Anurosporidium* Caullery & Chappellier, 1906.
Genus *Bertramia* C. & M., 1898.
Genus *Ichthyosporidium* C. & M., 1905.
Genus *Coelosporidium* M. & M., 1899.

This classification, taken from the first edition of Kudo's text, remained essentially unchanged throughout the five editions of his "Protozoology." The only significant change was the inclusion in the fifth edition (Kudo, 1966) of genus *Coleospora* Gibbs, 1959. In all editions the order was said to be characterized by the production of "simple spores."

Classification by Caullery, 1953

Class HAPLOSPOREA n.cl.
Order HAPLOSPORIDIA C. & M., 1899.
Family HAPLOSPORIDIIDAE C. & M., 1905.
Genus *Haplosporidium* C. & M., 1899.
Genus *Urosporidium* C. & M., 1905.
Genus *Anurosporidium* C. & C., 1906.
Genus *Nephridiophaga* Ivanić, 1937.
Genus *Physcosporidium* Awerinzeff, 1925.

The new class was regarded by Caullery (1953) as having an autonomous position near the SPOROZOA. The spores were still said to be of simple structure and to contain a uninucleate germ. As I have already pointed out (Sprague, 1966a), Caullery made a "most significant contribution by rejecting about 30 genera, most of which he considered to be fungi." We can now dismiss these from our minds when considering the classification of the haplosporidia.

Classification by Sprague, 1966a

Class HAPLOSPOREA C., 1953
Order HAPLOSPORIDIA C. & M., 1899
Family HAPLOSPORIDIIDAE C. & M., 1905.
Genus *Haplosporidium* Lühe, 1900.
Genus *Minchinia* Labbé, 1896.
Genus *Urosporidium* C. & M., 1905.
Family to be established.
Genus *Nephridiophaga* I., 1937.
Genus *Physcosporidium* A., 1925.

Appended to the classification were some genera and species of uncertain systematic position thought to be possibly haplosporidia and one unnamed haplosporidian. This classification differs in only a few respects from that of Caullery (1953). At the familial level it separates the genera into two groups. At the generic level it adds genus *Minchinia* which, as I have pointed out (Sprague, 1963), was erroneously rejected by Debaisieux (1920). It excludes genus *Anurosporidium* because Dollfus (1925, 1946), finding tails on spores of the type species, rejected it as a junior synonym of *Urosporidium*.

Classification by Sprague, 1970

Subphylum IV. MICROSPORA S., 1969.
Class 2. HAPLOSPOREA C., 1953.
Order 1. HAPLOSPORIDA C. & M., 1899.
Family 1. HAPLOSPORIDIIDAE C. & M., 1905.
Genus *Haplosporidium* Lühe, 1900.
Genus *Minchinia* Labbé, 1896.
Genus *Urosporidium* C. & M., 1906.
Family 2. NEPHRIDIOPHAGIDAE n. fam.
Genus *Nephridiophaga* I., 1937.
Genus *Physcosporidium* A., 1925.

The scheme just outlined, being the latest and having evolved from previous ones, provides a convenient starting place for making deletions, additions, and other changes that are consistent with present knowledge and concepts.

First, I suggest that we reject family NEPHRIDIOPHAGIDAE. Its members were originally assigned to the HAPLOSPORIDA only because they have "simple" spores, although they have no known positive characters that suggest affinities to the typical haplosporidia. Genus *Physcosporidium* has only one species, *P. dallyelliae,* described by Awerinzew in 1925 and never reported again. The author noted a striking similarity of the spores to those of microsporidia, which they may well be. Genus *Nephridiophaga* contains several species. Before any electron microscope study was made on a typical haplosporidian, Woolever (1966) did an electron microscope study on *N. blattellae* (Crawley, 1905) Woolever, 1966, a species very much like the type. She demonstrated none of the positive characters that were later found to be distinctive for the typical haplosporidia. I urge that in future revisions of the classification we include only forms with positive characters that suggest affinities to the typical forms. Otherwise stated, we should reject from the haplosporidia all species that cannot be accepted with no better justification than that they have "simple" spores and do not obviously belong to another group. Accordingly, I propose that we reject the genus *Coleospora* Gibbs, 1959, which was accepted by Kudo (1966).

There are two genera which we must consider adding to the classification. One is *Marteilia* Grizel, Comps, Bonami, Cousserans, Duthoit, and Le Pennec, 1974. Perkins (1976) says he has already "shown to be a member of the protozoan class Haplosporea." He reasons, "the presence of haplosporosomes in plasmodia and spores, sporoplasm delimitation by internal cleavage, and formation of spores from plasmodia all indicate affinities of *M. refringens* with the Haplosporea." In addition, the multicellularity of the spores is consistent with the idea of Cépède (1911) and Ormières et al. (1973) that typical haplosporidia have multicellular spores. Since there are positive characters linking *Marteilia* to the haplosporidia, I feel this genus should be included in the classification. Because of striking differences from

the typical forms, such as the great complexity of its spores, this genus should form the basis for a new taxon of high rank. The other genus that may have affinities to the haplosporidia is *Paramyxa* Chatton, 1911. This genus (with a single species) is the sole basis of the order PARAMYXIDA Chatton, 1911. The spore is a complex structure consisting of a sporoplasm enveloped by a parietal cell. The sporoplasm is binucleate but one nucleus degenerates. Chatton (1911) considered *Paramyxa paradoxa* to be a cnidosporidian with an abortive cnidocyst represented by the degenerating nucleus in the sporoplasm. During the present process of revising the classification of the protozoa, Levine[1] (manuscript handed out at this symposium) suggested that this organism become the basis of a new class in the haplosporidia. Perhaps we now see the beginning of a trend toward grouping with the "simple" sporidia complex protists that are not obviously something else. However, I am favorably impressed with Levine's suggestion (footnote 1) because of increasing evidence that the haplosporidian spore, like that of *Paramyxa* consists of cell(s) within cell(s). (It has already been suggested by Cépède (1911) and Chatton (1911), respectively, that HAPLOSPORIDA and PARAMYXIDA are similar to MYXOSPORIDA; interestingly, the circle has now been completed by the suggestion of Levine (footnote 1) that PARAMYXIDA and HAPLOSPORIDA are similar.) My inclination is to accept Levine's suggestion because it is consistent with our changing concept of the haplosporidia while, at the same time, I can find no compelling reason to reject it.

When we revise the classification I propose that we restore the genus *Anurosporidium* Caullery and Chappellier, 1906. This genus was rejected by Dollfus (1925, 1946) because the spores do have tails, originally overlooked and presumed to be absent. I have studied (Sprague, 1970) these spores in slides given to me by Dollfus. The tails, 1-3 in number, are hyaline, inconspicuous, amorphous extentions of the exospore cytoplasm. Tails on the spores of typical species of *Urosporidium* are single, conspicuous in light microscopy, show complex structure in electron microscopy (Perkins, 1971; Ormières et al., 1973; Perkins et al., 1975) and have an architecture that differs with the species (Perkins et al., 1977).

Already it has been suggested by Sprague (1977) and Levine (footnote 1) that the haplosporidia be regarded as an independent group of protists and elevated to phylum rank. Finding suitable names for the new phylum and any other new taxa of high rank is a problem we must now face. Perhaps courtesy requires us to consider using the phylum name ACNIDOSPORA Cépède, 1911, since this name has already been used for a taxon including HAPLOSPORIDA and its presumed relatives. However, I favor rejecting it because it refers only to a negative character that is better not mentioned.

I feel strongly that the name of the phylum should not be derived from the generic name *Haplosporidium* because the root that means "simple" is most inappropriate. When naming taxa above those of the family group we should follow the principle of adopting names that are both appropriate and have reference to positive characters. Furthermore, since we are not bound by a law of priority regarding these names, I propose that we take this opportunity to replace the inappropriate names HAPLOSPOREA Caullery, 1953, and HAPLOSPORIDA Caullery and Mesnil, 1899, with appropriate ones. (Roots for forming the new names suggested below are taken from Jaeger, 1944.)

Proposed Modification of the Classification

Phylum IV. ASCETOSPORA ph. n.
(ascet- Gr. asketos, curiously wrought. Refers to the strange and complex spore structure, recently revealed with the electron microscope.) Spore multicellular (or unicellular?), with one or more sporoplasms, without polar capsules or filaments; parasitic.

Class 1. STELLATOSPOREA nom. n. pro HAPLOSPOREA Caullery, 1953.
(stellat- L. stellatus, speckled. Refers to the speckled appearance of the cytoplasm in some stages due to the presence of "haplosporosomes" as seen in electron micrographs.) Haplosporosomes present. Spore with one or more sporoplasms.

Order 1. OCCLUSOSPORIDA Perkins, ord. n.
(occlus- L. occlusus, shut up. Refers to the enclosure of one sporoplasm within another. This name is attributed to Perkins because, in an unpublished manuscript[2], he considered the root to be accurately descriptive of the only genus in the order.) Spore with more than one sporoplasm. Sporulation involves a series of endogenous buddings, producing sporoplasm(s) within sporoplasm(s). Spore wall entire.

Family 1. MARTEILIIDAE fam. n.
With characters of the order.
Genus *Marteilia* Grizel, Comps, Bonami, Cousserans, Duthoit, and Le Pennec, 1974. (This genus may be sufficiently different from typical haplosporidia as to belong in a separate class. However, to avoid unnecessary proliferation of high level data, I place it only in a separate order now.)

Order 2. BALANOSPORIDA nom. n. pro HAPLOSPORIDA C. & M., 1899.
(balan- Gr. balanos, acorn. Refers to a stage in sporogenesis that resembles an acorn in its cupule.) Spore with one sporoplasm. Spore wall interrupted anteriorly by an orifice. Orifice covered externally with an operculum or internally by a diaphragm.

[1] Levine, N. D., College of Veterinary Medicine, University of Illinois, Committee on Systematics and Evolution of the Society of Protozoologists. A new revised classification of the protozoa. Unpubl manuscr., 65 p.

[2] Perkins, F. O. 1975. Virginia Institute of Marine Science, Gloucester Point, VA 23062 *Occlusosporidium aberum* gen. n., sp. n. (Sporozoa: Haplosporida) - causative agent of Aber disease in French oysters. Unpubl. manuscr., 8 p.

Family 1. HAPLOSPORIDIIDAE C. & M., 1905.

Spore with operculum.

Genus *Haplosporidium* C. & M., 1899.

Genus *Minchinia* Labbé, 1896.

Family 2. UROSPORIDIIDAE n. fam.

Spore without operculum, the orifice being covered internally by a diaphragm ("lingua").

Genus *Urosporidium* C. & M., 1905.

Genus *Anurosporidium* C. & C., 1906.

Class 2. PARAMYXEA Levine, cl. n.

Spore bicellular, consisting of a parietal cell and one sporoplasm; without orifice.

Order 1. PARAMYXIDA Chatton, 1911.

With characters of the class.

Genus *Paramyxa* Chatton, 1911.

[Note added in proof. Desportes and Ginsburger-Vogel (1977), which appeared after the preparation of this paper, stated that *Marteilia* is related to MYXOSPORIDA, ACTINOMYXIDA and PARAMYXIDA. I do not insist that the position I have taken regarding the taxonomic issues involved is preferable to that taken by Desportes and Ginsburger-Vogel. I feel that more information is needed before the issues can be resolved.]

Literature Cited

Awerinzew, S. 1925. Untersuchungen ueber parasitische Protozoen. VIII. *Physcosporidium dallyeilliae* n.g. n. sp. Russk. Arkh. Protist. Moscow 3:105-115.

Caullery, M. 1953. Appendice aux Sporozoaires: Classe des haplosporidies (Haplosporidia Caullery et Mesnil 1899). Traité de Zoologie I(2):922-934.

———, and A. Chappellier. 1906. *Anurosporidium pelseneeri* n.g., n. sp., Haplosporidie infectant les sprocysts d'un trematode parasite de *Donax trunculus* L. C. R. Seances Soc. Biol. Fil. 60:325-328.

———, and F. Mesnil. 1899a. Sur le genere *Aplosporidium* (nov) et l'ordre nouveau des Aplosporidies. C. R. Seances Soc. Biol. Fil., Ser. 1, 51:789-791.

———, and ———. 1899b. Sur les *Aplosporidies*, order nouveau de la classe des Sporozoaires. C. R. Acad. Sci., Paris 129:616-619.

———, and ———. 1905. Recherches sur les haplosporidies. Arch. Zool. Exp. Gen., Ser. IV, 4:101-181.

Cépède, C. 1911. Le cycle évolutif et les affinités systématiques de l'Haplosporidie des Donax. C. R. Acad. Sci., Paris 153:507-509.

Chatton, E. 1911. Sur une Cnidosporidie sans cnidoblaste (*Paramyxa paradoxa* n.g., n. sp.). C. R. Acad. Sci., Paris 152:631-633.

Corliss, J. O. 1974. The changing world of ciliate systematics: Historical analysis of past efforts and a newly proposed phylogenetic scheme of classification for the protistan phylum ciliophora. Syst. Zool. 23:91-138.

Debaisieux, P. 1920. *Haplosporidium (Minchinia) chitonis* Lank., *Haplosporidium nemertis*, nov. sp., et le groupe des Haplosporidies. Cellule 30:293-311.

Desportes, I., and T. Ginsburger-Vogel. 1977. Affinités du genre *Marteilia*, parasite d'Huîtres (maladie des Abers) et due Crustacé *Orchestia gammarellus* (Pallus), avec Myxosporidies, Actinomyxidies et Paramyxidies. C. R. Acad. Sci., Paris 285:1111-1114.

Dollfus, R. 1925. Liste critique descercaires marines a queue setigere signalees jusqu'a present. Travaux de la Station Zoologique de Wimereux, t. 9:3-65.

———. 1946. Parasites internes de Trematodes. *In* P. Lechevalier (editor), Encyclopédie biologique 27:16-36. Paris.

Grizel, H., M. Comps, F. Cousserans, J. R. Bonami, and C. Vago. 1974. Etude d'un parasite de la glande digestive observé au cours de l'épizootie actuelle de l'huître plate. C. R. Acad. Sci., Paris 279:783-784.

———, ———, J. R. Bonami, F. Cousserans, J. L. Duthoit, and M. A. Le Pennec. 1974. Recherche sur l'agent de la maladie de la glande digestive de *Ostrea edulis* Linné. Sci. Pêche 240:7-30.

Honigberg, B. M. (chairman). 1964. A revised classification of the phylum protozoa. J. Protozool. 11:7-20.

Jaeger, E. C. 1944. A source-book of biological names and terms. Charles C. Thomas, Springfield, Ill., 256 p.

Kudo, R. R. 1931. Handbook of protozoology. Charles C. Thomas, Springfield, Ill., 451 p.

———. 1966. Protozoology. 5th ed. Charles C. Thomas, Springfield, Ill., 1174 p.

Lom, J. 1969. Notes on the ultrastructure and sporoblast development in fish parasitizing myxosporidian of the genus *Sphaeromyxa*. Z. Zellforsch. Mikorsk. Anat. 97:416-437.

———, and J. O. Corliss. 1967. Ultrastructural observations on the development of the microsporidian protozoon *Plistophora hyphessobryconis* Schaperclaus. J. Protozool. 14:141-152.

———, and J. Vávra. 1962. A proposal to the classification within the subphylum Cnidospora. Syst. Zool. 11:172-175.

Lühe, M. 1900. Ergebnisse der neueren Sporozoenforschung, Zusammenfassende Darstellung mit besonderer Berücksichtigung der Malariaparasiten und ihrer nächsten Verwandten. *In* Centralblatt fur Bakteriologie, Parasitlenkunde and Infektionskrankheiten 28:384-392.

Mackin, J. G., and H Loesch. 1954. A haplosporidian hyperparasite of oysters. Proc. Natl. Shellfish. Assoc. 45:182-183.

Ormières, R., V. Sprague, and P. Bartoli. 1973. Light and electron microscope study of a new species of *Urosporidium* (Haplosporida), hyperparasite of trematode sporocysts in the clam *Abra ovata*. J. Invertebr. Pathol. 21:71-86.

Perkins, F. O. 1971. Sporulation in the trematode hyperparasite *Urosporidium crescens* de Turk, 1940 (Haplosporida: Haplosporidiidae)—an electron microscope study. J. Parasitol. 57:9-23.

———. 1976. Ultrastructure of sporulation in the European flat oyster pathogen, *Marteilia refringens*—Taxonomic implications. J. Protozool. 23:64-74.

———, P. A. Madden, and T. K. Sawyer. 1977. Ultrastructural study of the spore surface of the haplosporidian *Urosporidium spisuli*. Trans. Am. Microsc. Soc. 96:376-382.

———, and P. H. Wolf. 1976. Fine structure of *Marteilia sydneyi* sp. n.—haplosporidan pathogen of Australian oysters. J. Parasitol. 62:528-538.

———, D. E. Zwerner, and R. K. Dias. 1975. The hyperparasite, *Urosporidium spisuli* sp. n. (Haplosporea), and its effects on the surf clam industry. J. Parasitol. 61:944-949.

Schewiakoff, H. 1893. Veber einige ekto-und endoparasitische Protozoen der Cyclopiden. Bull. Soc. Nat. Moscow, No. 1.

Sprague, V. 1963. Revision of genus *Haplosporidium* and restoration of genus *Minchinia* (Haplosporidia, Haplosporidiidae). J. Protozool. 10:263-266.

———. 1965. Some problems in taxonomy and nomenclature of the Haplosporidia. Prog. Protozool. Proc. Int. Congr. Protozool. Ser. 91:125-126.

———. 1966a. Some problems relevant to biology and taxonomy of Haplosporidia. *In* A. Corradetti (editor), Proc. First Int. Congr. Parasitol. 1:449-450. Pergamon Press, Lond.

———. 1966b. Suggested changes in "A revised classification of the phylum protozoa," with particular reference to the position of the Haplosporidans. Syst. Zool. 15:345-349.

———. 1969. Need for drastic revision of the classification of subphylum Amoebogena. Prog. Protozool. IIIrd Int. Congr. Protozool., 372 p.

———. 1970. Recent problems of taxonomy and morphology of haplosporidia. [Abstr. 602.] J. Parasitol. 56:327-328.

———. 1977. Systematics of the microsporidia. *In* L. A. Bulla, Jr. and T. C. Cheng (editors), Comparative pathobiology, vol. 2, 510 p. Plenum Press, N.Y.

Stoll, N. R. (chairman). 1961. International code of zoological nomenclature. International Commission on Zoological Nomenclature, Lond., 176 p.

Vávra, J. 1966. Some recent advances in the study of microsporidian spores. *In* A. Corradetti (editor), Proc. First Int. Congr. Parasitol. 1:443-444. Pergamon Press, Lond.

Woolever, P. 1966. Life history and electron microscopy of a Haplosporidian, *Nephridiophaga blattellae* (Crawley) n. comb., in the Malphigian tubules of the German cockroach, *Blattella germanica* (L.). J. Protozool. 13:622-642.