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Factors affecting the size of spores of Myxidium zealandicum Hine, 1975 (Protozoa : Myxosporida)

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Factors affecting the size of spores of *Myxidium zealandicum* Hine, 1975 (Protozoa : Myxosporida)

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Variations in the size and shape of *Myxidium zealandicum* spores were not related to cyst size or host size, but variation was apparent between host species and individual fish. Spores from *Anguilla australis* were larger (7.9–15.3 μm long) and more uniform in shape than the small (6.1–11.7 μm long) irregularly shaped spores from *A. dieffenbachii*. Spore size was also consistent between cysts in individual *A. australis*, but variable between cysts in *A. dieffenbachii*. Abnormal spores were rare in *A. australis*, but more common and associated with small arcuate spores in *A. dieffenbachii*.

It is proposed that size and shape are genetically determined but may be highly modified by the biochemistry/physiology of the host at the site of sporogony. *A. australis* is a more suitable host for *M. zealandicum* than *A. dieffenbachii*, and constancy in spore size between cysts in *A. australis* was attributed to plasmotomy prior to sporogony. Spore valve striation numbers are genetically determined and variable, but no trends in variation were discernable. Cyst shape may be of taxonomic use within a host species, but not between host species.

INTRODUCTION

The limitations to the use of the spore in myxosporidan taxonomy have long been realised, and attempts have been made to fully utilise the morphological features of this stage (Lom 1969a, Donetz & Shulman 1973). The disadvantages have been compounded by the large number of studies in which the sole description is based on little material from one host or site of infection, or without any observations on spore variation. In some genera (e.g., *Myxobolus*), species have been distinguished on the basis of very small differences in morphology or size, and Mitchell (1977) observed, "Species descriptions are based mostly on spore morphology and the validity of many species remains questionable".

Three species of *Myxidium* have been described from New Zealand eels (Hine 1975) (*M. zealandicum, M. serum,* and *M. acinum*). Subsequent study has shown that *M. zealandicum* infects many organs in *Anguilla australis* and *A. dieffenbachii,* and that the site of sporogony may effect spore size and maturity; variations in spore striation number and pattern were also observed, and it was thought that host species and cyst size might affect spore development (Hine 1978).

This study was carried out to investigate spore variation in relation to host species, host size, and cyst size in one site of infection, the gills, as a prelude to a study on other species of *Myxidium* infecting eels (*Anguilla* spp.).

MATERIALS AND METHODS

Longfin (*Anguilla dieffenbachii*) and shortfin (*A. australis*) eels were collected by electric fishing from Makara Stream (NZMS N164/282276) between December 1978 and March 1979, transported live to the laboratory, and overdosed with benzocaine. The gills were excised and examined individually. Cyst diameter and shape were recorded, and either air dried smears were made of their contents, or whole cysts were fixed in 3% glutaraldehyde. Air dried smears were stained with Giemsa improved R66 (Gurr), and spores were measured at ×1600 using a hairline micrometer on a Zeiss Universal microscope. Glutaraldehyde-fixed cysts were dehydrated in an ethanol series, dried by critical-point freezing, coated with gold, and examined on a Cambridge Mark 2A scanning electron microscope (SEM).

Giemsa stained smears were used instead of fresh spores so that direct comparisons could be made with fixed material from an earlier study (Hine 1978). By examining spores *in situ* in cysts under the SEM, problems of cross-contamination from other cysts were reduced. Details of samples are given in Table 1; from these, 6 *A. dieffenbachii* (212–478 mm long) and 7 *A. australis* (204–470 mm long), with large numbers of gill cysts, were studied in detail.

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RESULTS

Spore Size

There was no obvious relationship between spore size and either cyst size or host size (Figs 1–4), but variation was apparent in relation to host species and between individual eels (Figs 1–4, Table 2). Spores from *A. australis* were larger than those from *A. dieffenbachii* (Fig. 1, Table 2), and spore size in individual eels was more consistent in *A. Australis* than in *A. dieffenbachii* (Figs 2 & 3).

Small spores from cysts in *A. dieffenbachii* were very similar in size and appearance to *Myxidium acinum* spores (Hine 1975) (Figs 3, 5 & 6, Table 2), and sometimes could be distinguished only by faint valve striations on spores presumed, therefore, to be *M. zealandicum*. Cysts containing spores of *M. acinum* were found only in *A. dieffenbachii* (Figs 3 & 5, Tables 2 & 3), in the same eels as cysts containing small *M. zealandicum* and *M. acinum*-like spores.

Spore-like structures with rounded apices, well developed polar capsules, and little or no apparent sporoplasm, also occurred in some cysts from *A. dieffenbachii* and one cyst from *A. australis* (Fig. 6, Table 3). These were considered abnormal rather than immature spores since *M. zealandicum* is disporoblastic, and although mature spores were often observed in pairs the abnormal spores were always dissociated from each other. In size and shape they resembled previously recorded unstriated spores (Hine 1978). These abnormal spores usually occurred in cysts in association with small *M. zealandicum* or *M. acinum*-like forms.

Table 1. Details of samples of eels *Anguilla* (spp.) from Makara Stream, Wellington, Dec 1978–Mar 1979 (*, 36 with gill infections, 7 with gill arch infections; +, 0.05–1.90 for gill infections, 0.15–0.90 for gill arch infections).

	A. australis	*A. dieffenbachii*
No. of eels examined	84	55
Size range (mm)	160–647	152–671
No. of eels infected	39*	32
% infected	46.4	58.2
No. cysts smears taken	186	151
No. cyst smears used for spore measurements	43	44
Range of cyst size max. diam. (mm)	0.05–1.90+	0.05–0.75
No. spores measured	1335	1470

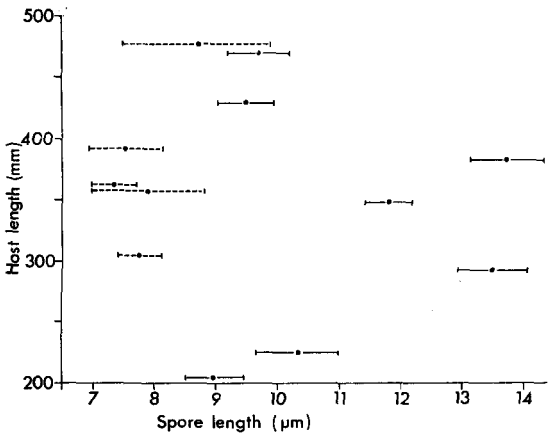
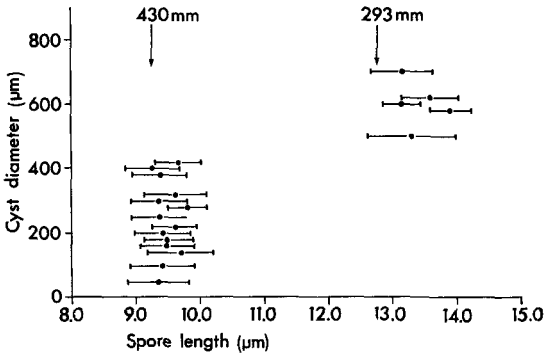


Fig. 1. Mean and standard deviation of *Myxidium zealandicum* spore length in relation to length and species of host (|——●——|, *Anguilla australis*; |----●----|, *A. dieffenbachii*).



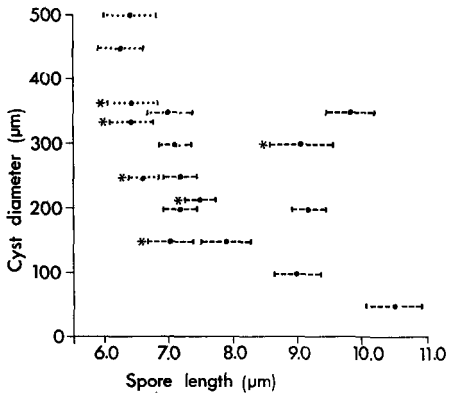


Fig. 2. (*Top*) Mean and standard deviation of *Myxidium zealandicum* spore length in cysts from two *Auguilla australis* (430 & 293 mm long) in relation to cyst diameter.

Fig. 3. (*Bottom*) Mean and standard deviation of spore lenth of *Myxidium acinum* (|····●····|), abnormal (|----●----|), and *M. zealandicum* (|----●----|) spores from two *Anguilla dieffenbachii* in relation to cyst diameter (*, host 478 mm long; no *, host 359 mm long).

Table 2. Length (L) and width (W) and ratios of dimensions of *Myxidium* spores from the gills and gill arches of *Anguilla australis* and *A. dieffenbachii* (S.D., standard deviation; —, not applicable)

	A. australis			*A. dieffenbachii*		
	Range	Mean	S.D.	Range	Mean	S.D.
M. zealandicum (gills)						
Length (μm)	7.9–15.3	11.42	±2.44	6.1–11.7	8.64	±1.43
Width (μm)	3.3– 7.4	4.87	±1.03	2.9– 5.7	4.37	±0.72
L:W ratio	0.26– 0.57	0.44	±0.04	0.32±0.69	0.56	±0.08
Abnormal spores						
Length (μm)	6.6– 8.4	7.55	±0.46	6.4– 8.9	7.20	±0.51
Width (μm)	4.4– 6.3	5.36	±0.48	3.5– 5.9	4.44	±0.57
L:W ratio	0.63– 0.84	0.71	±0.05	0.50– 0.75	0.61	±0.06
M. acinum						
Length (μm)	–	–	–	5.6– 7.7	6.56	±0.41
Width (μm)	–	–	–	2.8– 7.7	3.83	±0.31
L:W ratio	–	–	–	0.42– 0.86	0.59	±0.06
M. zealandicum (gill arch)						
Length (μm)	11.7–15.5	13.60	±1.01	–	–	–
Width (m)	4.1– 6.9	5.65	±0.61	–	–	–
L:W ratio	0.31– 0.57	0.43	±0.05	–	–	–

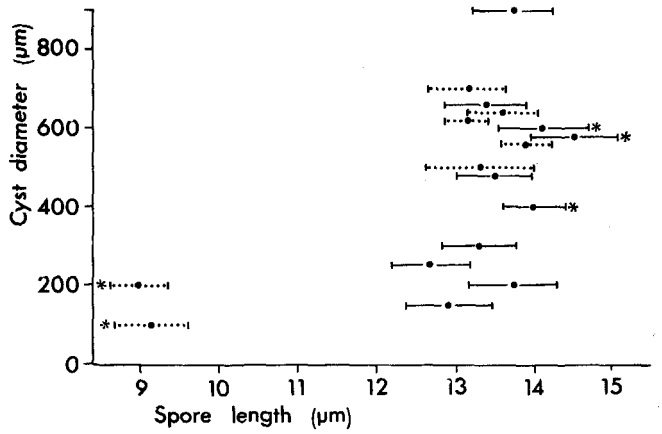


Fig. 4. Mean and standard deviation of spore length of *Myxidium zealandicum* spores from the gills (|·····●·····|) and gill arch (|——●——|) of two *Anguilla australis* in relation to cyst diameter (*, host 204 mm long; no *, host 293 mm long).

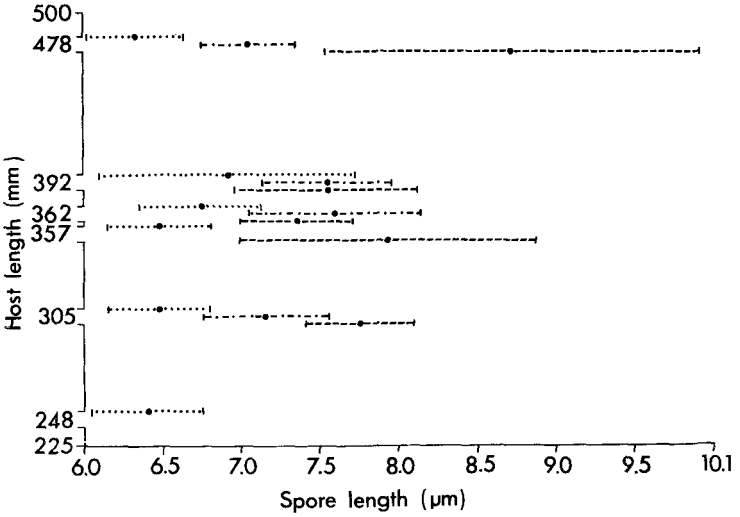


Fig. 5. Mean and standard deviation of spore length of *Myxidium acinum* (|···●···|) abnormal (|-----●-----|), and *M. zealandicum* (|----●----|) spores in relation to host length in *Anguilla dieffenbachii*.

	No. of *A. australis*	No. spores measured	No. of *A. dieffenbachii*	No. spores measured
M. zealandicum				
No. ± spherical cysts	41	1275	26	915
No. cigar-shaped cysts	1	30	1	30
Abnormal spores				
No. ± spherical cysts	1	30	4	120
No. cigar-shaped cysts	0	0	0	0
M. acinum				
No. ± spherical cysts	—	—	4	120
No. cigar-shaped cysts	—	—	9	285

Table 3. Occurrence of *Myxidium* spore types in relation to cyst shape in *Anguilla australis* and *A. dieffenbachii* (—, not applicable)

Gill arch infections were not seen in *A. dieffenbachii*, and although 7 out of 23 *A. australis* less than 350 mm long had cysts on the gill arch as well as the gills, none of 16 *A. australis* greater than 350 mm long were infected on the gill arch. Spores from gill arch cysts were larger than those from the gills (Table 2), except in one eel (293 mm long) in which spores from gill cysts were also large and similar to gill arch spores in size (Fig. 4).

Table 4. Numbers and widths of surface striations on spores from cysts in *Anguilla australis* and *A. dieffenbachii* (S.D., standard deviation).

Eel length (mm)	Striation no.		Striation width (μm)
A. australis	Range	Mean ± S.D.	Range
224	11–15	13.4 ± 1.2	0.2–0.5
293	12–17	14.0 ± 1.5	0.2–0.4
382	16–20	17.3 ± 1.7	0.2–0.3
430	9–16	13.0 ± 1.5	0.2–0.4
Total	**9–20**	**14.0 ± 2.1**	**0.2–0.5**
A. dieffenbachii			
359	10–14	12.9 ± 1.1	0.2–0.3

SHAPE

Cyst shape: Cysts were of two shapes; (a) spherical to sub-spherical or ovate, intralamellar, or (b) cigar-shaped intracapillary cysts running along the gill filament (Fig. 7 A–C). *A. australis* were infected with the first type, but one cigar-shaped cyst 1.9 mm long was found. Of the 10 cigar-shaped cysts observed in *A. dieffenbachii*, 9 contained *M. acinum* spores (Table 3). *M. zealandicum* was therefore usually associated with spherical cysts, and *M. acinum* with cigar-shaped cysts.

Spore shape: Within cysts, individual fish, and host species, small spores were wider in relation to length than large spores (Figs 8 & 9). Spore width was usually less than half the length in *A. australis*, but more than half the length in *A. dieffenbachii* (Fig. 10, Table 2). Large spores in both hosts were straight, fusiform, and radially symmetrical, whereas small spores, particularly in *A. dieffenbachii*, were arcuate or reniform, but bilaterally symmetrical in the plane of the sutural ridge (Fig. 6). In smears this gave an asymmetrical appearance similar to that of *M. acinum*, or species of the genus *Zschokkella* Auerbach, 1910. Apices were more attenuated in large than in small spores.

STRIATIONS

Valve striation numbers varied within and between cysts (Table 4), so that there was no obvious difference in numbers of striae in relation to cyst size, host size or species, or site of infection. The number of striae was not related to spore size, but striations were more pronounced on spores with few striations than on those with many (Fig. 7 D–F). Strands similar to those observed crossing the circumsutural furrow in *Myxosoma cerebralis* (Lom & Hoffman 1971) were observed crossing the striae in some cysts.

Variations also occurred in striation arrangements or patterns both within and between cysts (Fig. 7 D–F). Although no basic pattern could be discerned, some patterns were common in the cysts examined, and resembled those observed on *M. zealandicum* spores from the gills of *A. rostrata* in Canada (Komourdjian *et al.* 1977, figs 12–15).

DISCUSSION

The extremes of large, slim, straight, radially symmetrical spores of *Myxidium zealandicum* from *Anguilla australis*, and the small, arcuate or reniform, asymmetrical spores from *A. dieffenbachii*, are sufficiently different to be mistaken for two species. However, large spores from *A. dieffenbachii* and small spores from *A. australis* are indistinguishable, and until laboratory transmission proves otherwise, *M. zealandicum* must be considered a species showing very wide variation in spore shape and size. Small *M. zealandicum* spores from *A. dieffenbachii*

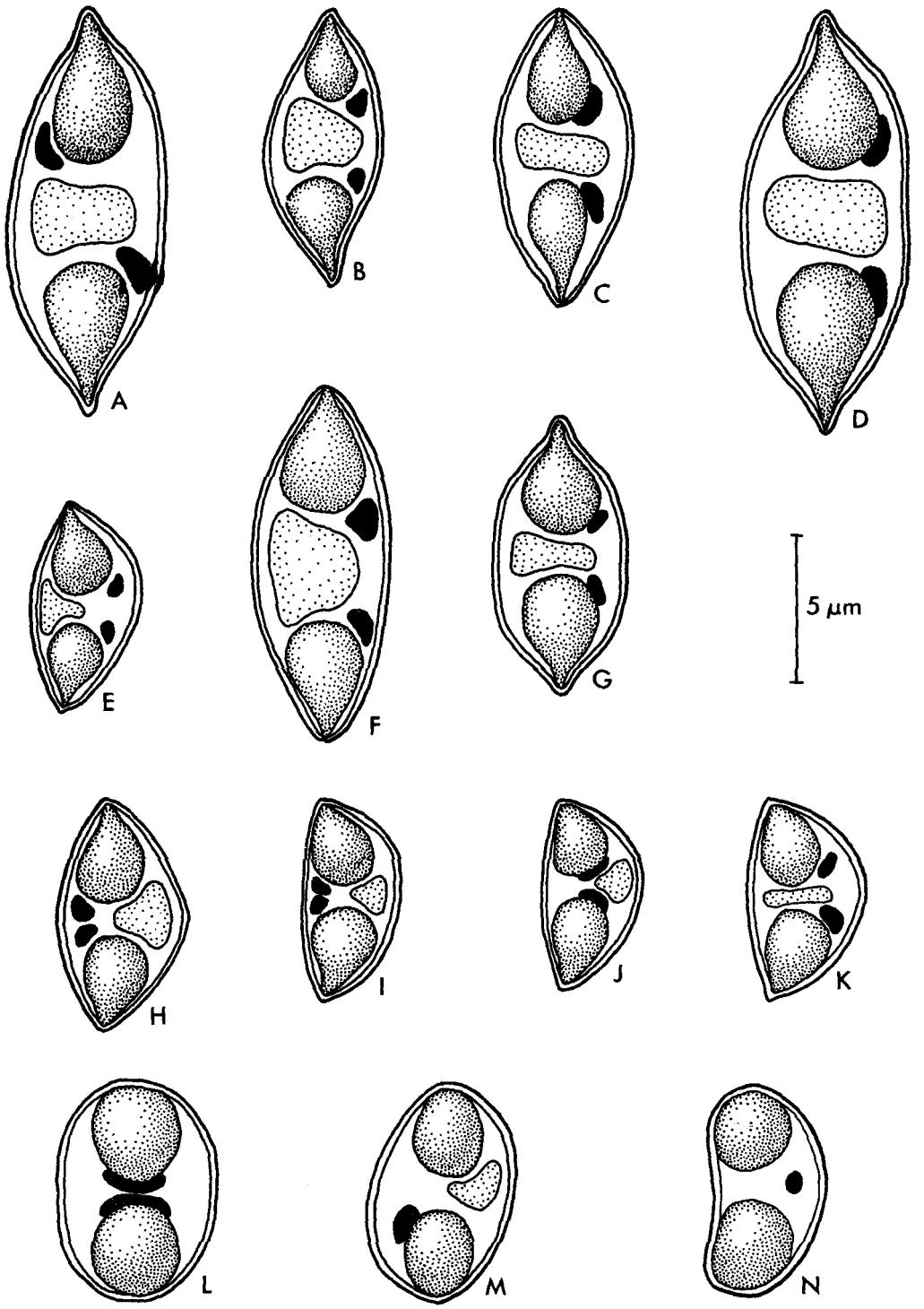
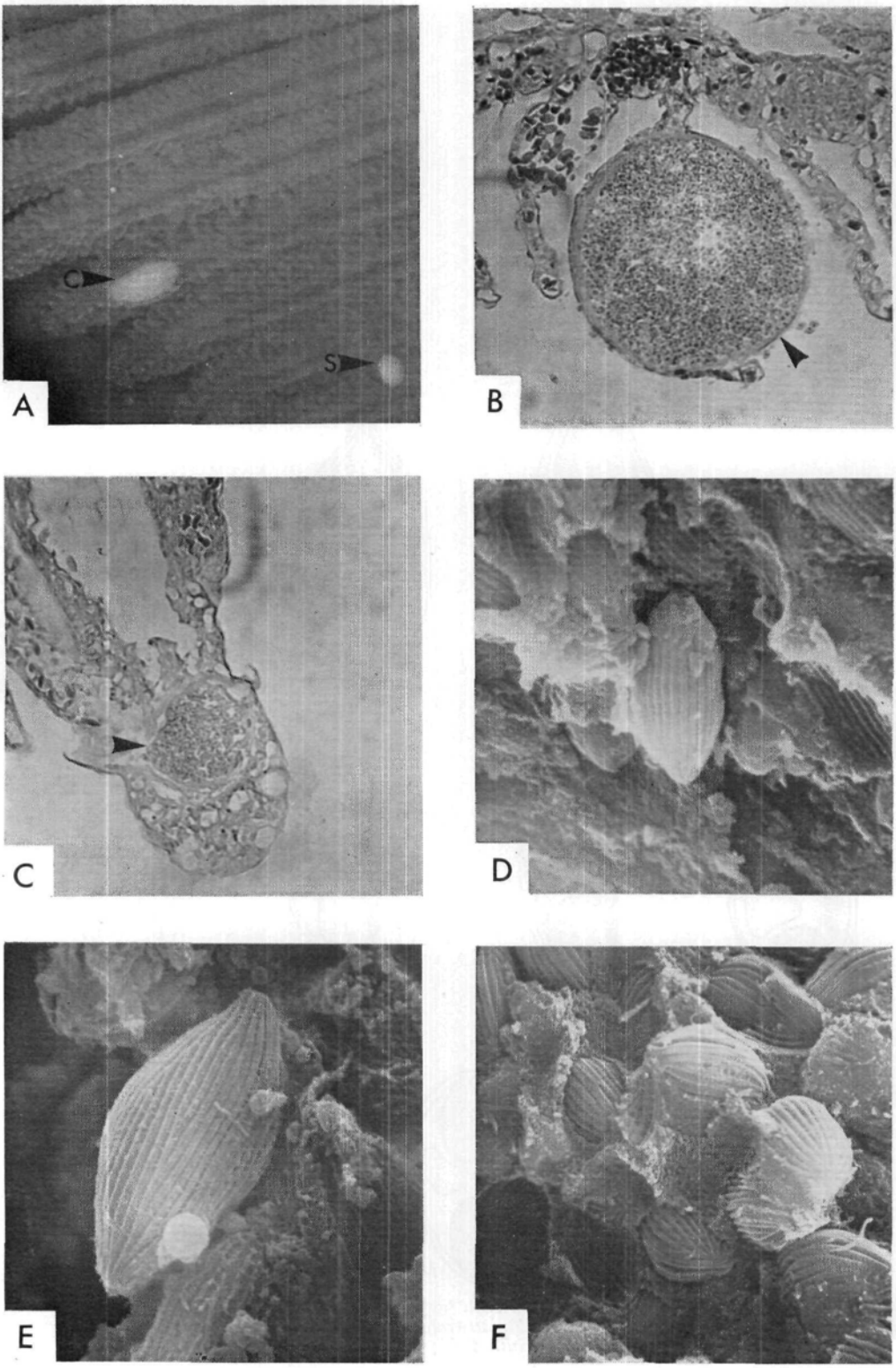


Fig. 6. Variation in appearance of spores from both hosts. A–C: *Myxidium zealandicum*, gills, *Anguilla australis;* D: *M. zealandicum*, gill arch, *A. australis;* E–I: *M. zealandicum*, gills, *A. dieffenbachii;* J & K: *M. acinum*, gills, *A. dieffenbachii;* L–N; abnormal spores.



may closely resemble *M. acinum* spores, and were found in association with abnormal spores. However, more typical *M. zealandicum* spores were often seen in the same cyst as abnormal and *M. acinum*-like spores, whereas *M. acinum* spores were uniform in appearance within the cyst. They are, therefore, considered to be two species although in the light of the variation reported here for *M. zealandicum*, further confirmation is desirable. *M. serum* reported from *A. dieffenbachii* by Hine (1975) falls within

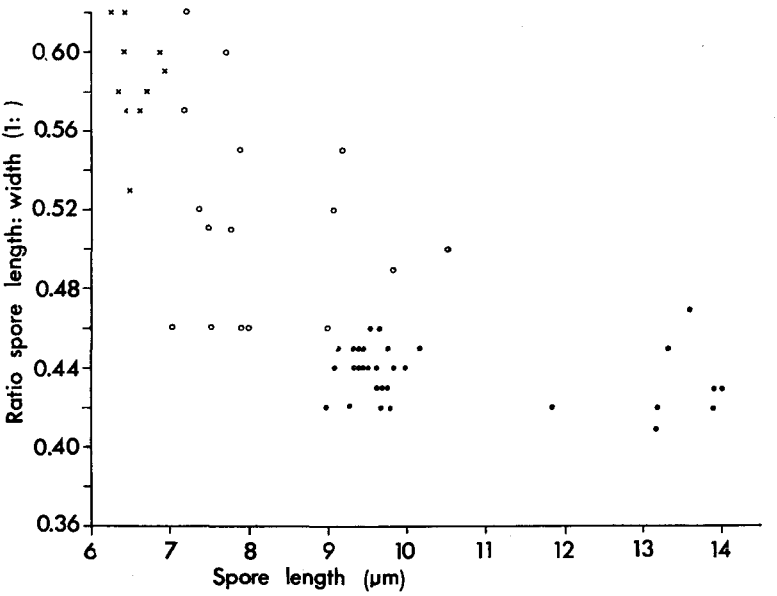


Fig. 8. Ratio of spore length: width, in relation to mean spore length from cysts containing *Myxidium acinum* (×), abnormal spores (O), and *M. zealandicum* (•). Data from both hosts.

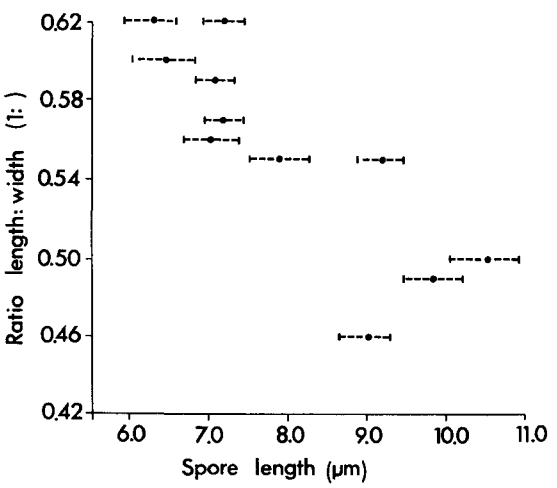


Fig. 9. Ratio of *Myxidium zealandicum* spore length: width in relation to mean spore length from cysts within one *Anguilla dieffenbachii* 478 mm long.

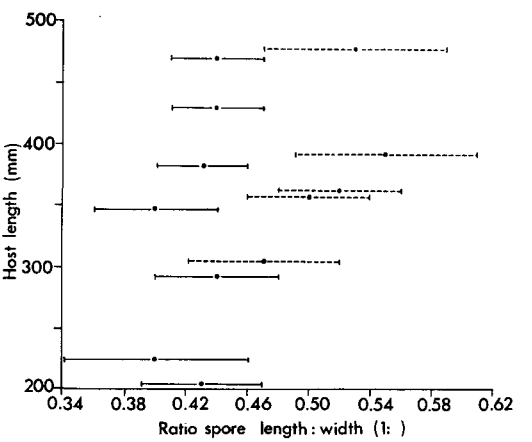


Fig. 10. Ratio of *Myxidium zealandicum* spore length: width in relation to host length in *Anguilla australis* (|——•——|), and *A. dieffenbachii* (|----•----|).

Fig. 7. (*opp.*) A: Cigar-shaped (C) and spherical (S) cysts; B: spherical cyst in section, *Anguilla australis;* C: cigar-shaped cyst in section, *A. dieffenbachii;* D, E, & F: SEM photographs of *Myxidium zealandicum* spores in *A. australis* (D & E), and *A. dieffenbachii* (F).

the size range of *M. zealandicum* from *A. australis*, and requires further taxonomic study.

Differences in size, shape, and constancy of size in the two hosts call into question the factors or mechanisms controlling these morphometric parameters. Moser (1977) proposed that in Myxosporida, (a) spore size is determined by factors located primarily within the host (i.e., confines of space), (b) spore shape is determined by the presence of physiologically and behaviourally suitable fish hosts, and (c) there is a constancy in spore size that is independent of geographical location, water depth, or season. To support (a) he compared spore dimensions of histozoic and coelozoic species, showed that coelozoic spores tend to be larger, and concluded that space is an important factor. The second point is an extension of Donets' (1969) observation that there is a relationship betwen spore settling rates and the specific host. Moser (1977) considered that shape is critical in determining spore settlement rates in the water column and is selected to maximise the time over which the host might ingest spores. Unfortunately his experimental evidence is not convincing, since it would apply only to fish in still bodies of water, and insufficient is known of myxosporidan transmission to predict the method of entry into the host. The most studied myxosporidan species, *Myxosoma cerebralis*, may be transmitted from infected mud, and aging of spores may enhance transmission (Hoffman & Putz 1971).

Moser's (1977) propositions are based on evolutionary selective processes acting on the parasite gene pool, i.e., his use of terms such as 'natural selection', 'selective pressure', and 'random drift' suggests that size and shape are genetically fixed. However, the data presented here and previously (Hine 1978) suggest that spore shape, size, and maturity are largely determined by the biochemical and/or physiological suitability of the environment in which the parasite develops — or more specifically in which sporogony occurs — in interaction with the genetic characteristics of the parasite. This suitability will vary with the site of sporogony, host species, and the biochemical/physiological status of the host. This confirms an earlier observation (Hine 1978) that degree of development and spore size were related to the site in which sporogony occurred. In the present study, spore size and shape varied between and within host species, and in individual fish. Also spore size was related to the site of infection (i.e., gill arch spores were generally larger than gill spores).

The small, bent spores and abnormal spores from *A. dieffenbachii*, and the longer uniform spores and rarer abnormal spores in *A. australis*, suggest that the latter may be a more suitable host for *M. zealandicum*. The lack of gill arch cysts in *A. australis* over 350 mm long may indicate that some biochemical or physiological change at this infection site makes the site unsuitable for sporogony in larger eels.

The confines of space at the site of sporogony might affect spore size, but great variation in size was observed between *M. zealandicum* in intralamellar cysts in different eels in which the restraints imposed by surrounding tissues would seem to be the same. Cyst shape or position within one host species may be of taxonomic value as the site of sporogony can determine cyst shape (Minchew 1973), and the differences in sites of sporogony may reflect differences in the biochemical/physiological requirements of the parasite species. Thus in *A. dieffenbachii*, *M. zealandicum* spores were, with one exception, found in spherical or sub-spherical cysts, whereas *M. acinum* spores were more often found in cigar-shaped cysts. However, in different hosts with concomitant differences in biochemistry and/or physiology, cyst shape and position are probably of no taxonomic value. Cysts containing *M. zealandicum* spores in the gills of *A. rostrata* (Komourdjan *et al.* 1977, fig. 6) were very different in position and shape from *M. zealandicum* cysts in gills of *A. australis* and *A. dieffenbachii*. Furthermore, there appear to be structural differences between the gills of different species of *Anguilla* (pers. obs.).

Of particular interest is the constancy of spore size seen in different gill cysts from individual *A. australis*. This may be interpreted in three ways.

(a) Spore size consistency results from intraspecific competition selecting for size when a large number of trophozoites infect *A. australis*. In *A. dieffenbachii*, infection by fewer trophozoites does not lead to competition and therefore size is determined by site suitability, resulting in the establishment of a variety of genotypes. However, similar numbers of cysts were observed in both species of eel, and only light infections were observed in both these hosts.

(b) Each cyst represents a different trophozoite, but the biochemical/physiological characteristics of the host gills are uniform and play an exclusive role in determining spore size, so that there is a constancy in spore size from cyst to cyst irrespective of genetic factors in the parasites. Thus biochemical/physiological factors *per se* determine spore size. This, however, does not seem likely as considerable variation in spore size was observed between cysts in the gills of individual *A. dieffenbachii*, and it is unlikely and inconsistent that biochemical/physiological variations sufficient to affect spore size would exist within small areas of the gills of the other eel species.

(c) One trophozoite forms daughter trophozoites by plasmotomy prior to sporogony; thus each cyst contains identical genetic material, and sporogony under similar biochemical/physiological conditions results in spore size constancy. This is supported by an observed constancy in the staining characteristics of spores of similar size from these cysts. Cysts containing a variety of spore sizes had different spore staining characteristics. It is suggested therefore, that trophozoites in *A. australis* may undergo plasmotomy before sporogony, whereas this is less common or does not occur in the less suitable host, *A. dieffenbachii*.

In summary, Moser (1977) proposed that size and shape are environmentally selected. Internal factors, notably confines of space, select for size; external factors, notably the behaviour and physiology of the host, select for shape. From the date collected in this and an earlier study (Hine 1978), it is suggested that size and possibly shape are strongly influenced by genotype but may be modified by the suitability of the site of sporogony. Multiplication of genetically identical trophozoites through plasmotomy is suggested as the cause of spore size consistency in *A. australis*. The critical factors at the site of sporogony are thought to be biochemical/physiological factors contributing nutrients to, or disposing of, the metabolic wastes of the cyst, and that availability of space is of relatively little importance. Ultrastructural studies have shown close connections between plasmodia and the host (Lom & de Puytorac 1969, Lom 1969b, Desser & Patterson 1978), and microvilli characterise the plasmodial membrane of *M. zealandicum* (Hulbert *et al.* 1977).

No trends were noticed in variation in striation number; striation numbers and patterns are probably genetically determined and not influenced by biochemical/physiological factors that modify shape and size.

Studies on *M. zealandicum* suggest that characters often used in myxosporidan taxonomic studies (i.e., spore size and shape, and cyst shape) may be far more variable and less indicative of species than previously thought. Furthermore, descriptions based on material from one cyst, one fish, or one host species may be misleading and inadequate, and result in a proliferation of species of dubious validity.

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