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LIFE HISTORY, PATHOLOGY, AND DESCRIPTION OF *KUDOA OVIVORA* N. SP. (MYXOZOA, MYXOSPOREA): AN OVARIAN PARASITE OF CARIBBEAN LABROID FISHES

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ABSTRACT: We describe *Kudoa ovivora* n. sp. from ovaries of bluehead wrasse, *Thalassoma bifasciatum,* and record its presence in 6 species (Labroidei) collected in the San Blas Islands, Panama. *Kudoa ovivora* spores are quadrate with rounded edges in apical view, oval-shaped with apical valve extensions in side view (mean spore dimensions: length 6.5 μm, width 7.7 μm, thickness 6.9 μm; mean polar capsule dimensions: length 2.1 μm, width 1.5 μm). This is the first *Kudoa* species from gonads of fishes. Prevalence of infection varied among labrids (*Thalassoma bifasciatum, Halichoeres bivittatus, Halichoeres garnoti, Halichoeres poeyi*), with *T. bifasciatum* exhibiting the greatest prevalence. Density of infection, measured as percent infected eggs, also varied among species with highest densities occurring in *H. garnoti. Kudoa ovivora* may not require an intermediate host because fishes fed infected tissue developed more infections than unfed fish. Infected eggs are inviable and larger and heavier than uninfected eggs. Infected eggs contain more organic and inorganic material, indicating that *K. ovivora* increases resource allocation to eggs. Therefore, infected females may have reduced growth, fecundity, and/or spawning activity. Because males were uninfected and all identified hosts are protogynous sequential hermaphrodites, further studies of *K. ovivora* may provide new insights on the costs/benefits of sex change.

Species of the class Myxosporea Buetschli, 1881 are parasites primarily of aquatic vertebrates, with the great majority infecting teleost fishes (Lom, 1987; Lom and Dyková, 1992). Most myxosporean infections result in mild host reactions, although heavy infections can result in high mortality due to effects such as whirling disease (Halliday, 1976; Hoffman, 1990) and proliferative kidney disease (Kent and Hedrick, 1986).

Until recently, the Myxosporea and the Actinosporea Noble, 1980 were considered separate classes in the phylum Myxozoa Grassé, 1970. Two major discoveries have resulted in a dramatic revision of the taxonomy of the phylum. First, molecular phylogenetic and ultrastructural analyses have determined that the Myxozoa are not a protozoan phylum, but a metazoan phylum related to either the Bilateria phyla (Smothers et al., 1994; Schlegel et al., 1996) or the phylum Cnidaria (Siddall et al., 1995), supporting the reasoning of Weill (1938). Second, Wolf and Markiw (1984) found evidence suggesting that myxosporeans and actinosporeans actually represent 2 stages of development in a complex parasite life cycle. Spores of the myxosporean *Myxobolus cerebralis* Hofer, 1903, when fed to a tubificid worm, *Tubifex tubifex,* resulted in an infection of a *Triactinomyxon* sp., a member of the Actinosporea. When *Triactinomyxon* spores were fed to a salmonid, an infection of *M. cerebralis* was initiated. Further attempts to document the phenomenon for other species have provided mixed results. Evidence for a myxosporean/actinosporean life cycle has currently been found for 17 myxosporean species in the following 7 genera: *Ceratomxyxa* Thélohan, 1892, *Hoferellus* Berg, 1898, *Myxidium* Buetschli, 1882, *Myxobolus* Buetschli, 1882, *Sphaerospora* Thélohan, 1892, *Thelohanellus* Kudo, 1933, and *Zschokkella* Auerbach, 1910 (see Kent et al., 1994; Upenskaya, 1995; Lom et al., 1997; McGeorge, Sommerville, and Wootten, 1997; Yokoyama, 1997). For these species, none of the myxosporean stage hosts is strictly a marine fish and all the actinosporean stage hosts are freshwater oligochaetes (Kent et al., 1994) or freshwater polychaetes (Bartholomew et al., 1997). Evidence for direct transmission in myxosporeans has been claimed for species in the genera *Myxobolus* and *Sphaerospora* (see Kent et al., 1994) and recently documented for *Myxidium* from a strictly marine fish host (Diamant, 1997). To date, there is no information on mode of transmission in the myxosporean genus *Kudoa* Meglitsch, 1947, to which the species described here belongs.

There are 45 described species of myxosporeans in the genus *Kudoa* and an additional 4 identified but undescribed species (see Appendix). Whereas there are several species in other myxosporean genera that infect the gonads of marine and freshwater fishes (e.g., Walliker, 1969; Paperna, 1973; Sitja-Bobadilla and Alvarez-Pellitero, 1990; Torres et al., 1994), this is the first record of a *Kudoa* species infecting reproductive tissue.

While studying egg viability in Caribbean coral reef fishes, we observed and collected conspicuously colored white eggs from several free-spawning labrids that produce pelagic eggs (*Thalassoma bifasciatum* Bloch, 1791, *Halichoeres bivittatus* Bloch, 1791, *Halichoeres garnoti* Valenciennes, 1839, and *Halichoeres poeyi* Steindachner, 1867). Upon examination, we determined that the eggs were infected with an unknown species of *Kudoa.* Here, we describe a new myxosporean species, *Kudoa ovivora* n. sp., from the ovaries of the bluehead wrasse, *T. bifasciatum* (Labridae). We also report the results of a direct transmission experiment to determine if *K. ovivora* can be transmitted via the ingestion of infected eggs. We follow the guidelines of Lom and Arthur (1989) in preparing this description and report the presence of *K. ovivora* in 3 additional species of labrids and 3 species of scarids, their sister taxon.

MATERIALS AND METHODS

Prevalence of infection

To estimate prevalence of infection, we either netted or speared fish specimens in the spring and summer of 1993 and 1996 on coral reefs near the Smithsonian Tropical Research Institute field station in the San Blas Islands, Panama (see Robertson [1987] for map). We collected females by lift net from 0900 to 1100 hr, prior to the onset of spawning, and brought them to the field station where we placed them in holding nets in the sea to allow eggs to hydrate (cf. Warner, 1985; Schultz and Warner, 1989). Beginning at 1400 hr, we lightly anesthetized each female (5–10 sec) in a bucket containing dilute Quinaldine in seawater, rinsed them, and measured their standard lengths (SL, to the nearest

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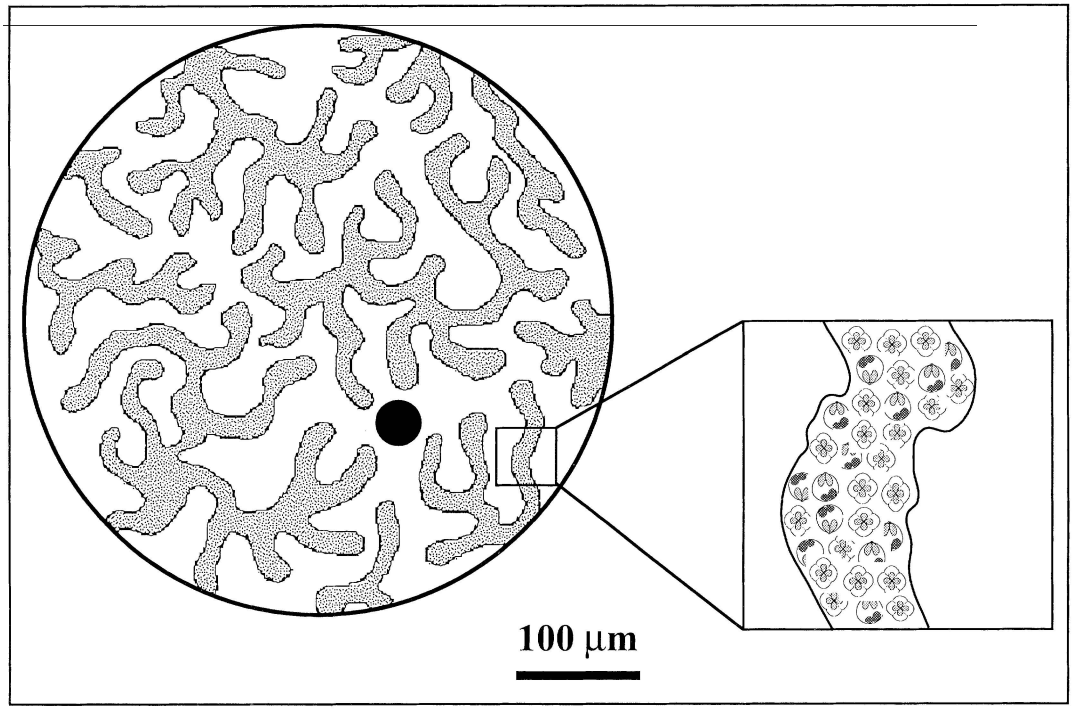

FIGURE 1. Line drawing of an infected *Thalassoma bifasciatum* egg illustrating the arrangement of plasmodia within the egg (black circle, oil droplet; enlargement, plasmodium containing mature spores).

mm). Then, we gently squeezed the abdomen of each female, and, if gravid, we expressed the eggs into a petri dish containing distilled water (eggs sink in distilled water which facilitates counting and evaluation). For females collected with microspears (90 cm × 3 mm steel rods powered by handheld rubber bands), we also measured them (SL) and expressed any ripe egg clutches into 5-ml vials containing seawater within 15 min of capture. We immediately placed the samples on ice and brought them to the field station for analysis. To determine the presence of infected eggs, we visually inspected eggs from both netted and speared females under a dissecting scope. To determine the percentage of infected eggs, we counted 200 randomly chosen eggs from each egg clutch. If less than 200 eggs were present, we counted all eggs present.

We recorded the prevalence of infection in wild-caught females, as determined by the production of white eggs, for 4 species, *T. bifasciatum, H. bivittatus, H. garnoti,* and *H. poeyi.* We also determined presence of infection in 3 other species, *Sparisoma rubripinne* Valenciennes, 1840 from a wild-caught female, and *Sparisoma aurofrenatum* Valenciennes, 1840 and *Sparisoma radians* Valenciennes, 1840 from histological preparations provided by R. Warner. These ovarian thin sections were obtained from individuals collected in San Blas in 1975 during a study of the sexuality of these species (Robertson and Warner, 1978). To test for differences in the prevalence of infection among species, we compared the proportion of infected females for the 4 labrid species (*T. bifasciatum, H. bivittatus, H. garnoti, H. poeyi*) using a Tukey-type multiple-comparisons test of proportions (Zar, 1996).

We determined density of infection, measured as the percentage of eggs infected within a clutch, for 3 of the 7 species, *T. bifasciatum, H. bivittatus,* and *H. garnoti.* We tested for differences among the 3 species in the percentage of eggs infected using a nonparametric multiple-comparisons test with unequal sample sizes and tied ranks (Zar, 1996). For *T. bifasciatum,* we tested whether the probability of infection increases with increased size by regressing the arcsine-transformed proportion of infected females against female size class. We calculated the regression statistics using the software package DataDesk 5.01 (Velleman, 1995).

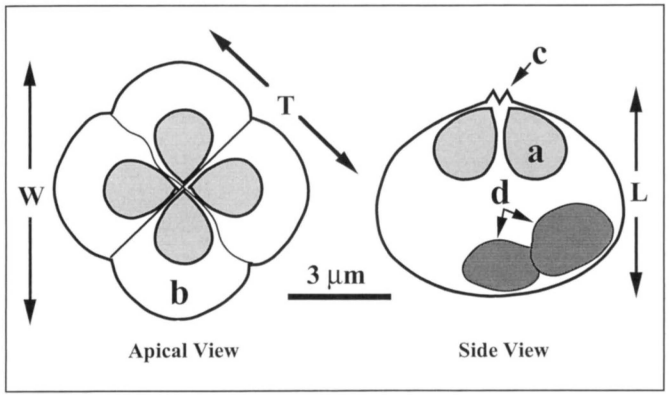

FIGURE 2. Diagram of a *Kudoa ovivora* spore with dimensions: W, width; T, thickness; L, length. Additional spore features: a, polar capsule; b, shell valve; c, apical projection; d, nuclei (note unequal size).

Occurrence of *Kudoa ovivora* in different tissues

To assess which tissues are infected by *K. ovivora,* we froze both male and female *T. bifasciatum* for microscopic examination. We inspected wet mounts of dorsal musculature, spleen, kidney, liver, intestine, nervous tissue, testis, and ovary under 1,250× magnification using an Olympus BH2 light microscope with a differential interference contrast attachment for the presence of spores.

Parasite morphology

To determine the number, arrangement, and shape of the whitish cysts (plasmodia-containing spores), we expressed infected ripe eggs from gravid females into petri dishes containing distilled water and viewed them under a dissecting microscope. For detailed histological examination of the morphology of *K. ovivora* plasmodia, we preserved infected ovaries in Dietrich's fixative. Then, we thin-sectioned the ovaries, mounted the tissue onto slides, and stained each slide with hematoxylin and eosin. We viewed these histological preparations under 400× magnification.

We observed and measured spores from frozen infected *T. bifascia-*

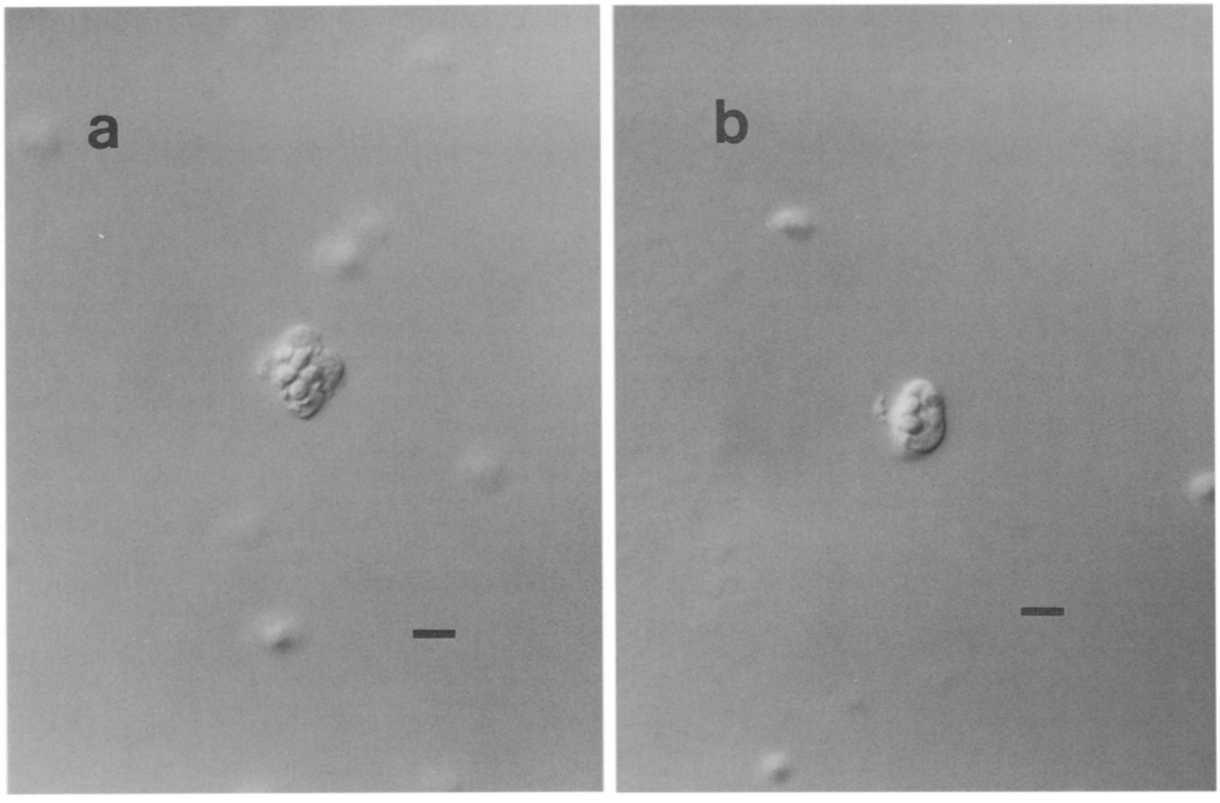

FIGURE 3. *Kudoa ovivora* spore in (a) apical view and in (b) side view. Scale bar = 4 μm (wet mount, phase contrast).

tum eggs in wet mount preparations following Lom (1969) to determine spore size and shape. We measured 10 spores/host (6 for spore length) from 6 fish (n = 60, 36 for spore length) using a calibrated ocular micrometer under 1,250× magnification using an Olympus BH2 light microscope with phase-contrast illumination. We lysed and ultrasonified additional infected eggs to release spores from the plasmodia for scanning electron microscopy (SEM). These spores were dehydrated in 75% ethanol, critical point dried, gold sputter coated, and examined with a JEOL JSM-5300LV at 15 kV. We tested for within- and between-host variation in spore dimensions using a 1-way analysis of variance (ANOVA). We performed this test using DataDesk 5.01 (Velleman, 1995).

Mode of transmission

To evaluate whether *K. ovivora* can be transmitted directly via the ingestion of infected eggs, we collected female *T. bifasciatum* from 1 reef following the same methods described above (Prevalence of infection). This experiment was motivated by our field observations of individuals feeding on infected eggs during the spawning period. We stripped females of their eggs and, if the clutch was free of white-colored eggs, we randomly placed each female in 12-gallon aquaria (6 females/aquarium) equipped with bricks and small lengths of PVC tubing for shelter. We netted additional females from 2 reefs to collect infected eggs and ovaries. We fed infected eggs and macerated ovary from females with infected eggs to fish in the 5 experimental aquaria on the first 2 days after initial capture. We observed some fish feeding on the infected tissue. The control aquaria consisted of fish that we did not feed infected tissue. For the duration of the experiment (1 mo), we fed fish in the 10 aquaria (5 experimental and 5 control treatments) daily on oven-dried macerated anchovies. We flushed each tank 4 times/day using a gravity flow-through seawater system.

After 1 mo, we preserved the surviving individuals in Dietrich's fixative. Subsequently, we thin-sectioned the ovaries, mounted the tissue onto slides, and stained the slides with hematoxylin and eosin following the methods of Humason (1972). We observed the prepared histological thin sections under 400× magnification for the presence of spores. For the individuals with active ovaries that have eggs in developmental stages known to have spores, we tested for differences in the presence of infection between the exposed and unexposed treatments using a binomial test (Zar, 1996). We also tested for differences in mortality rates between the 2 treatments using a Mann–Whitney *U*-test (Zar, 1996).

Pathology

To determine the effect of *K. ovivora* infections on egg performance, we conducted artificial fertilization experiments on uninfected and infected eggs to assess the viability of infected eggs. We stripped ripe eggs from females into 250-ml glass jars filled with seawater. If both infected and uninfected eggs were present, we immediately expressed sperm from a male and gently swirled the jar to facilitate sperm and egg mixing and allowed the samples to stand for at least 2 hr before observation. We then transferred samples to petri dishes filled with distilled water and evaluated both infected and uninfected eggs for fertilization success (cell division in the form of a blastodisc). We evaluated 100 uninfected eggs and all infected eggs from each egg clutch from a total of 10 clutches. We tested for differences in fertilization success between the 2 egg types using a χ^2 test (Zar, 1996).

To determine the relative energetic investment into infected eggs, we measured egg diameters, egg dry weights, and egg ash (inorganic) and ash-free (organic) dry weights of infected eggs, uninfected eggs from infected females, and uninfected eggs from uninfected females. We stripped eggs from infected (n = 12) and uninfected females (n = 10) into petri dishes containing seawater and measured egg diameters using a calibrated ocular micrometer attached to a dissecting scope at 40× magnification. We measured 10 eggs/female for a minimum of 100 measurements/egg type (except for 2 of the infected females that had <10 infected eggs each).

For dry weight measurements, we separated egg clutches from 28 infected females and 31 uninfected females by egg type and transferred each sample to 1.5-ml vials in which they were rinsed with distilled water and freeze dried. Samples from each female consisted of approximately 50 eggs to ensure measurable sample weights. We measured dry weights using a Cahn 28 Microbalance and standardized these

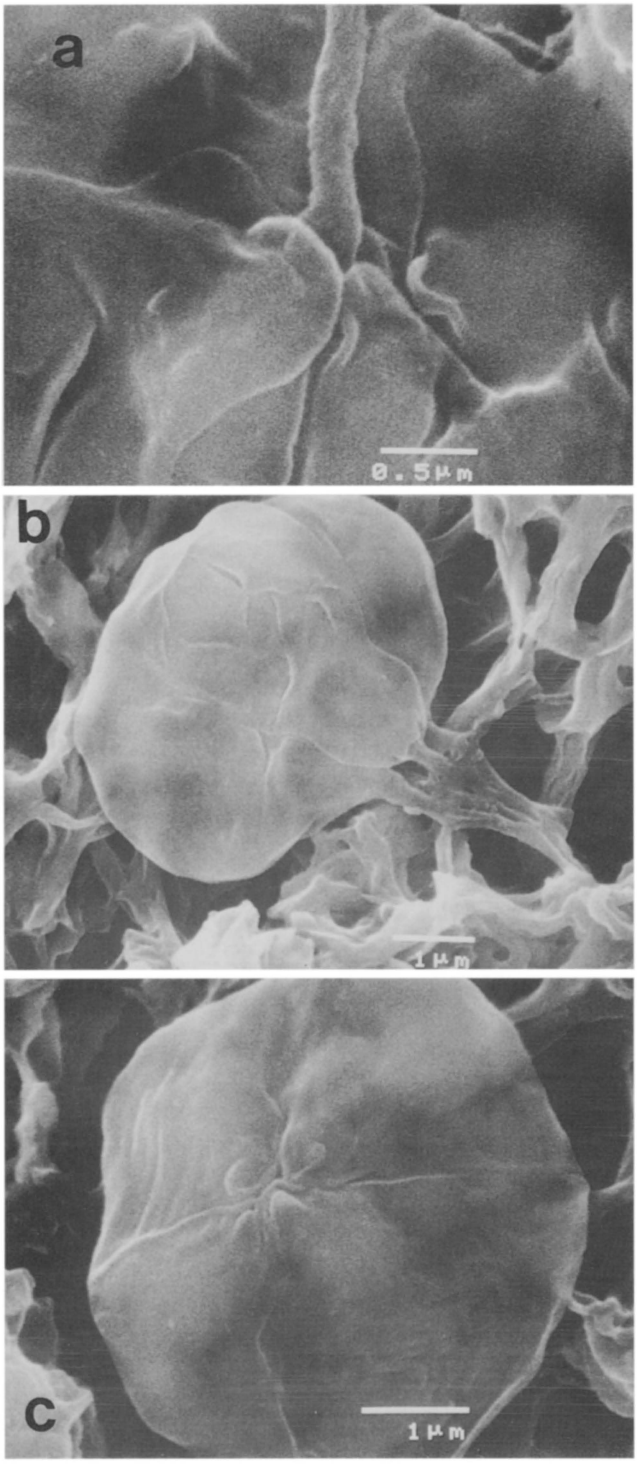

FIGURE 4. Scanning electron microscopy (SEM) of *Kudoa ovivora* spores: (a) apical projections with extruded polar filament, (b) side view, and (c) apical view.

weights by egg number to determine mean egg dry weight for each sample.

To determine ash (inorganic) dry weight and ash-free (organic) dry weight, we transferred eggs from infected (n = 12) and uninfected females (n = 7) to 1.5-ml vials, rinsed each sample with distilled water, and freeze dried them. We determined sample dry weights using the same methods as above. We then transferred each sample onto an aluminum foil boat that had been previously ashed for 1 hr to stabilize its weight. We ashed these samples in a Blue M Co. Lab-Heat model muffle furnace at 450–550 C for 4 hr and then allowed them to cool before reweighing.

We tested for differences in egg diameter and egg dry weight among infected eggs, uninfected eggs from infected females, and uninfected eggs from uninfected females using Tukey multiple-comparisons tests (Zar, 1996). We assessed differences in ash weight and ash-free dry weight between infected and uninfected eggs using *t*-tests (Zar, 1996).

Taxonomic affinity

To comprehensively compare *K. ovivora* to other *Kudoa* species, we compiled a database of the taxonomic and descriptive characteristics of all currently described species (see Appendix). From this database, we generated the following 12 variables: Site of infection (fins, gall bladder, gills, heart, mesentery, musculature, nervous tissue, ovary, or urinary tract), number of spores per trophozoite (mono-, di-, or polysporous), spore shape in apical view (ovate, quadrate, or stellate), spore length rank, spore width rank, spore thickness rank, polar capsule shape (ovate, pyriform, or elongate), polar capsule size (equal or unequal), polar capsule length rank, polar capsule breadth rank, apical valve extensions (presence or absence), and lateral valve extensions (presence or absence). We used these 12 variables to calculate dissimilarity coefficients for each pairwise species comparison following the method of Kaufman and Rousseeuw (1990). For mixed variables (binary, interval-scaled, and nominal), the dissimilarity coefficient =

$$\sum_{f=1}^{p} \delta_{ij}^{(f)} d_{ij}^{(f)} \Big/ \sum_{f=1}^{p} \delta_{ij}^{(f)}$$

For both the binary and nominal variables (f): $d_{ij}^{(f)} = 1$ if $x_{if} \neq x_{jf}$ or 0 if $x_{if} = x_{jf}$ and $\delta_{ij}^{(f)} = w_{ij}^{(f)}$ when x_{if} and x_{jf} are both nonmissing or 0 if 1 or both are missing, where $w_{ij}^{(f)}$ = the probability of $x_{if} = x_{jf}$. We applied this weighting function to the model so that the dissimilarity coefficients would not be disproportionately influenced by variables which intrinsically, have a higher probability of being dissimilar, e.g., the probability of the site of infection variable being dissimilar is 0.9, whereas the polar capsule size probability is 0.5. For interval-scaled variables, $d_{ij}^{(f)} = |x_{if} - x_{jf}|/R_f$, where R_f is the range of the variable f. We then performed an average linkage cluster analysis of the dissimilarity matrix using the statistical software package SYSTAT (Wilkinson, 1989).

DESCRIPTION

Kudoa ovivora n. sp.
(Figs. 1–4)

The plasmodia (cysts containing spores) are tubular and branching in shape (25–50 µm in diameter) and coiled along the egg cell membrane (Fig. 1). Oocytes appear to be infected with multiple plasmodia. Plasmodia contain multiple spores (polysporous). Sporogenesis appears to be synchronous because plasmodia only contained mature spores and not mixtures of mature and immature spores.

Mature spores are quadrate with rounded edges in apical view (Figs. 2, 3a). Spores are oval-shaped in side view (Figs. 2, 3b). Lateral valve extensions are absent, but small apical projections are present (Fig. 4a). The surface of the spore is fairly smooth with lateral ridges (Fig. 4b). There are 2 visible suture lines separating the 4 shell valves. One suture line is straight, the other is slightly curved (Fig. 4c). The polar capsules are pyriform in shape and equal in size. They are arranged with the anterior ends close together but not overlapping. The number of polar filament coils could not be determined because the polar capsules were highly refractive. There is 1 sporoplasm with 2 nuclei located in the posterior portion of the spore. Spore measurements (mean [range]) are: length 6.5 (5.0–7.5) µm, width 7.7 (6.7–8.3) µm, thickness 6.9 (5.8–7.7) µm, polar capsule length 2.1 (1.7–2.5) µm, and polar capsule width 1.5 (1.3–1.7) µm.

There were no consistent differences in either spore length, width, or thickness among the 6 hosts used for spore morphological measurements. Spore dimensions were as variable within individual hosts as between hosts (Table I).

TABLE I. Effect of host on *Kudoa ovivora* spore dimensions (1-way ANOVA).*

Factor	Source of variation	SS	df	MS	F	*P*
Spore width	Total	11.357	59			
	Between hosts	1.245	5	0.249	1.330	0.27
	Error (within host)	10.112	54	0.187		
Spore thickness	Total	8.350	59			
	Between hosts	0.785	5	0.157	1.120	0.36
	Error (within host)	7.565	54	0.140		
Spore length	Total	7.069	35			
	Between hosts	1.389	5	0.278	1.467	0.23
	Error (within host)	5.680	30	0.189		

* SS = sum of squares; df = degrees of freedom; MS = mean squared deviation from the mean; F = between host MS/within host MS; *P* = probability.

Taxonomic summary

Type host: Thalassoma bifasciatum Bloch, 1791 (Labroidei, Labridae).

Other hosts: Halichoeres bivittatus Bloch, 1791, *H. garnoti* Valenciennes, 1839, *H. poeyi* Steindachner, 1867 (Labroidei, Labridae); *Sparisoma aurofrenatum* Valenciennes, 1840, S. radians Valenciennes, 1840, and *S. rubripinne* Valenciennes, 1840 (Labroidei, Scaridae).

Site of infection: Ovary, intracellular in oocytes.

Locality: San Blas Islands, Caribbean coast of Panama (9°34′N, 78°58′W).

Species evaluated for K. ovivora *infections and their localities (F = Florida Keys; P = Panama; S = St. Croix, U.S. Virgin Islands): Bodianus rufus* Linnaeus, 1758 (P), *Clepticus parrai* Bloch & Schneider, 1801 (P), *Halichoeres bivittatus* Bloch, 1791 (F, P), *H. garnoti* Valenciennes, 1839 (F, P, S), *H. maculapinna* Müller & Troschel, 1848 (F, P), *H. poeyi* Steindachner, 1867 (P), *Thalassoma bifasciatum* Bloch, 1791 (F, P, S) (Labroidei, Labridae); *Scarus iserti* Bloch, 1790 (F, P), *Sparisoma aurofrenatum* Valenciennes, 1840 (F, P), *S. radians* Valenciennes, 1840 (P, S), *S. rubripinne* Valenciennes, 1840 (F, P), *S. viride* Bonnaterre, 1788 (F), (Labroidei, Scaridae); *Acanthurus bahianus* Castelnau, 1855 (P), *A. coeruleus* Bloch & Schneider, 1801 (P) (Acanthuroidei, Acanthuridae); *Serranus tigrinus* Bloch, 1790 (P) (Percoidei, Serranidae).

Material deposited: Symbiotypes on slides: KOV1, thin section of infected *T. bifasciatum* ovary; KOV2, spores stained with hematoxylin and eosin. Frozen symbiotype: KOV3, *T. bifasciatum* eggs with spores. Slides and frozen eggs deposited in the Museum of Systematics and Ecology, Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, California.

Etymology: The name *ovivora* derives from ovum = egg, vora = consume. It refers to the fact that the parasite consumes eggs that it infects.

TABLE II. Prevalence of *Kudoa ovivora* infections in 7 species of Caribbean coral reef fish (n = number of females evaluated for infection).

Species	n	Number infected	Percent infected
Labridae			
Thalassoma bifasciatum 1996	1,038	416	40.1
Thalassoma bifasciatum 1993	406	93	22.9
Halichoeres bivittatus	106	5	4.7
Halichoeres garnoti	123	20	16.3
Halichoeres poeyi	19	1	5.3
Scaridae			
Sparisoma aurofrenatum	5	1	20.0
Sparisoma radians	16	6	37.5
Sparisoma rubripinne	1	1	—

Prevalence of infection

We found infected eggs to varying degrees in the 7 species examined (Table II). Among the 4 labrid species (*T. bifasciatum, H. bivittatus, H. garnoti,* and *H. poeyi*), we found significant differences in the percentage of infected females, with *T. bifasciatum* exhibiting the highest prevalence of infection (Table III). For *T. bifasciatum,* infected fish ranged in size from 37 to 86 mm SL and were, on average, significantly larger than uninfected fish (Mann–Whitney *U*: $z = -9.701$, $P < 0.0001$). In fact, the proportion of infected individuals increased with increasing size (Fig. 5).

The percentage of infected eggs within a clutch varied both among individuals of the same species as well as among the 3 primary species studied (Fig. 6). Generally, the infection within an individual was either limited to a few eggs (light infection) or was spread throughout most of the egg clutch (heavy infection). Among *T. bifasciatum, H. bivittatus,* and *H. garnoti,* we found significant differences in the proportion of eggs infected within a clutch, with *H. garnoti* exhibiting the heaviest levels of infection (Table IV); more than half the infected females had >70% of their eggs infected (Fig. 6).

Site of infection

White-colored plasmodia containing fully mature spores were restricted to the inner wall of the egg membrane (Fig. 7a, b), and we only observed spores in late developmental stage oocytes that had begun or completed vitellogenesis. We did not detect plasmodia in the dorsal musculature, spleen, kidney, liver, intestine, or nervous tissue from females with infected ovaries (n = 10). We also examined 25 males from 2 heavily infected populations on isolated patch reefs (>65% infected). For all 25 males, we found no spores in the testes or in any other tissue examined.

Mode of transmission

Of the 60 female *T. bifasciatum* used in the feeding exposure experiment, only 37 survived (38% mortality). However, there were no differences in the mortality rates between fed and unfed treatments (Mann–Whitney *U*: $z = 1.080$, $P = 0.28$). Of the 37 surviving females, only 11 (30%) had active ovaries that could be evaluated for the presence of *K. ovivora* spores. Based on these 11 individuals, 7 (88%) of the exposed females had *K. ovivora* infections, whereas 1 (33%) of the unexposed females was infected. Using 0.33 as the baseline probability of infection, females fed infected eggs and ovaries were significantly more likely to develop infections than expected without exposure ($F_{0.05(1),8,10} = 8.75$, $P < 0.0025$).

Pathology

Eggs infected with *K. ovivora* are not viable. All of the infected eggs (n = 1,623) we evaluated were unfertilized, whereas 98% of the uninfected eggs (n = 1,000) were successfully fertilized and showed normal cell development ($\chi^2 = 2{,}552$, df = 1, $P < 0.0001$). We saw no cell division in any of the infected eggs.

Also, there were differences in the size and weights of infected eggs relative to uninfected eggs from both infected and uninfected females

TABLE III. Results of a Tukey-type multiple-comparisons test for differences in the prevalence of *K. ovivora* infections among 4 labrid host species.*

Species	n	p'	Comparison	q	$q_{0.05,\infty,4}$	Conclusion
Thalassoma bifasciatum (1)	406	39.182	1 vs. 2	12.780	3.633	T.b.>H.b.
Halichoeres bivittatus (2)	106	12.840	1 vs. 3	8.102	3.633	T.b.>H.g.
Halichoeres garnoti (3)	123	23.559	1 vs. 4	5.316	3.633	T.b.>H.p.
Halichoeres poeyi (4)	19	14.568	3 vs. 2	4.001	3.633	H.g.>H.b.
			3 vs. 4	1.821	3.633	H.g.=H.p.
			4 vs. 2	0.346	3.633	H.p.=H.b.

* $p' = \frac{1}{2}[\arcsin\sqrt{X/n + 1} + \arcsin\sqrt{X + 1/n + 1}]$; $q = (p'_B - p'_A/SE$, SE, $= \sqrt{410.35/(n_A + 0.5) + 410.35/(n_B + 0.5)}$ where n_B and n_A = the number of females of each species in the comparison.

(Fig. 8a, b). Infected eggs were approximately 1.2× larger in diameter and 2.25× heavier than uninfected eggs, whereas there were no differences between uninfected eggs from infected and uninfected females in either size or weight (Table V). The difference in weight between infected and uninfected eggs reflected differences in both the organic and inorganic fractions of the egg (Fig. 8c). Both the ash dry weight (inorganic fraction) and ash-free dry weight (organic fraction) were more than 5× and 2× greater, respectively, in infected eggs compared to uninfected eggs from uninfected females (1-tailed *t*-tests: ash dry weight, $t = 1.975$, df = 17, $P = 0.03$; ash-free dry weight, $t = 4.989$, df = 17, $P < 0.0001$).

DISCUSSION

Taxonomic summary

Based on geographic location, spore dimensions, spore morphology, and site of infection, the myxosporean identified here is a new species of the genus *Kudoa* that we describe as *K. ovivora* (Fig. 2). Only 3 other species have been identified from the Caribbean: *Kudoa crumena* (Iverson and Van Meter, 1967), *Kudoa leiostomi* (Dyková et al., 1994), and *Kudoa shkae* (Dyková et al., 1994). All 3 species infect the musculature of non-reef-associated fishes (*Scomberomorus maculatus* Mitchill, 1815, *Leiostomus xanthurus* Lacépède, 1802, and *Arius felis* Jordan & Gilbert, 1883, respectively. Both *K. crumena* and *K. leiostomi* are larger than *K. ovivora,* and *K. shkae* lacks apical projections. *Kudoa crumena* and *K. shkae* are round instead of quadrate in apical view (see Appendix).

Seven described species of *Kudoa* have similar spore dimensions to those of *K. ovivora*: *Kudoa cascasia* (Sarkar and Chaudry, 1996), *Kudoa caudata* (Kovaleva and Gaevskaya, 1983), *Kudoa miniauriculata* (Whitaker et al., 1996), *Kudoa paniformis* (Kabata and Whitaker, 1981), *Kudoa sciaenae* (Teran, Llicán, and Luque, 1990), *K. shkae* (Dyková, Lom, and Overstreet, 1994), and *Kudoa tachysurae* (Sarkar and Mazumder, 1983). However, all but *K. shkae* are found in different

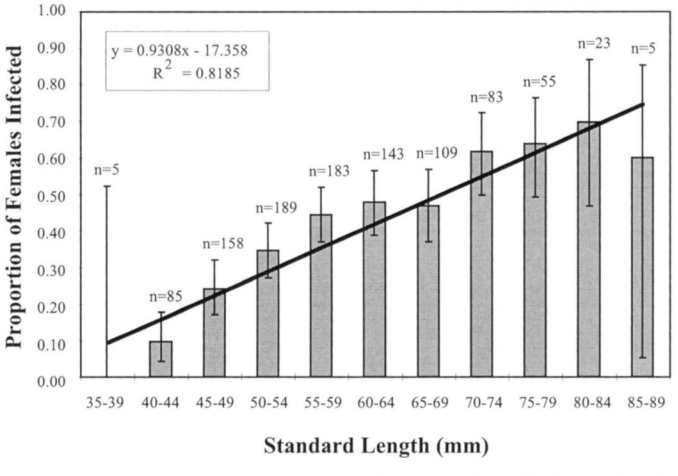

FIGURE 5. Frequency histogram of the proportion of infected female *Thalassoma bifasciatum* within each size class (n = number of females; total n = 1,038). Error bars are the 95% confidence limits for the proportion of infected females within each size class. The regression equation is for the arcsin-transformed data; $F = 40.595$, $P < 0.001$. The slope of the regression is significantly different from 0: $t = 6.3714$, $P < 0.001$. (Note: individuals become sexually mature at ~35 mm SL.)

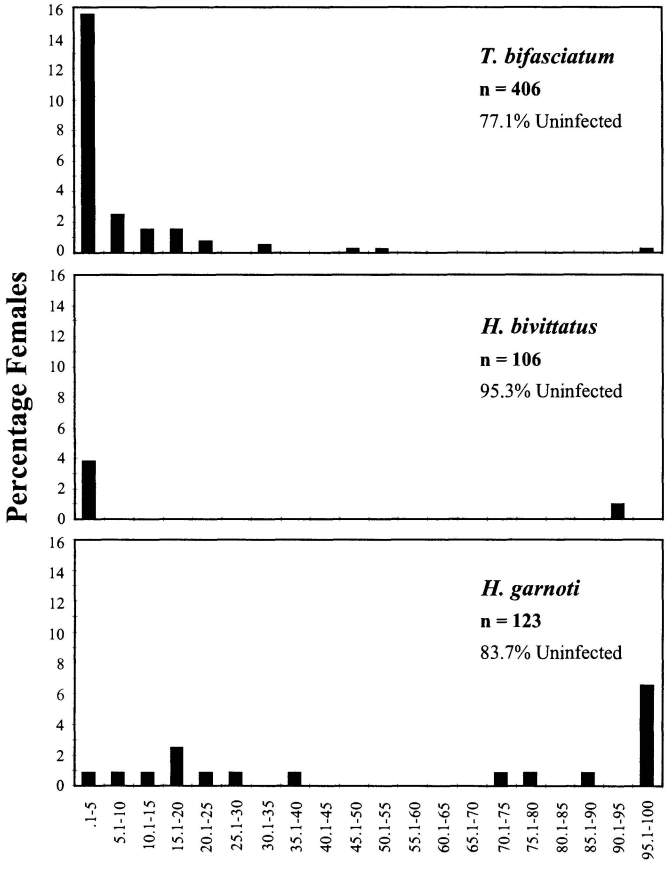

FIGURE 6. Density of infection of *Kudoa ovivora* in 3 species of Caribbean coral reef fish.

TABLE IV. Results of a Tukey-type nonparametric multiple-comparisons test for differences in the percentage of eggs infected among 3 labrid host species.*

Species	n	Mean rank	Comparison	Q	$Q_{0.05,3}$	Conclusion
Thalassoma bifasciatum (1)	93	49.2	3 vs. 1	6.011	2.394	H.g.>T.b.
Halichoeres bivittatus (2)	5	56.4	3 vs. 2	2.541	2.394	H.g.>H.b.
Halichoeres garnoti (3)	20	99.8	2 vs. 1	0.460	2.394	H.b.=T.b.

* Mean rank $(\bar{R}) = \Sigma_{i=1}^{n} R_i/n$; $Q = (\bar{R}_B - \bar{R}_A)/SE$, $SE = \sqrt{(N(N+1)/12 - \Sigma\, t/12(N-1)(1/n_A + 1/n_B)}$, where $N = \Sigma\, n$ for all three species, n_B and n_A = the number of females of each species in the comparison, and $\Sigma\, t = \Sigma_{i=1}^{m} (t_i^3 - t_i)$, where t = number of females with same rank and m = number of groups of tied ranks.

geographic localities, and all infect different tissue types than *K. ovivora.* Except for *K. cascasia,* they also have different spore morphologies compared to *K. ovivora. Kudoa caudata* and *K. miniauriculata* have lateral valve filaments and lateral valve extensions, respectively. *Kudoa sciaenae, K. shkae, K. tachysurae,* and *K. paniformis* all lack apical valve extensions. *Kudoa paniformis* is also round in apical view.

There are 7 species that are similar in shape to *K. ovivora*: *K. cascasia* (Sarkar and Chaudry, 1996, *Kudoa chilkaensis* (Tripathi, 1951), *Kudoa funduli* (Hahn, 1915; Meglitsch, 1947), *Kudoa intestinalis* (Maeno, Magasawa, and Sorimachi, (1993), *Kudoa iwatai* (Egusa and Shiomitsu, 1983), *K. leiostomi* (Dyková, Lom, and Overstreet, 1994), and *Kudoa pericardialis* (Nakajima and Egusa, 1978). Both *K. funduli* and *K. iwatai* are larger and *K. intestinalis* and *K. pericardialis* are smaller than *K. ovivora.* Again, all but *K. leiostomi* are found in different geographic regions and latitudes and all infect different tissues than *K. ovivora.* This combination of differences and the unique site of infection for this genus clearly distinguishes *K. ovivora* from all other known *Kudoa* species.

From the cluster analysis of the dissimilarity coefficients, there are 7 main groupings of *Kudoa* species that are defined by unique combinations of taxonomic characteristics (Fig. 9). Based on this analysis, *K. ovivora* is similar to *K. cascasia, K. leiostomi, K. funduli, K. chilkaensis, Kudoa cerebralis,* and *K. sciaenae.* This group is defined by moderately sized quadrate spores with apical extensions and equal-sized pyriform polar

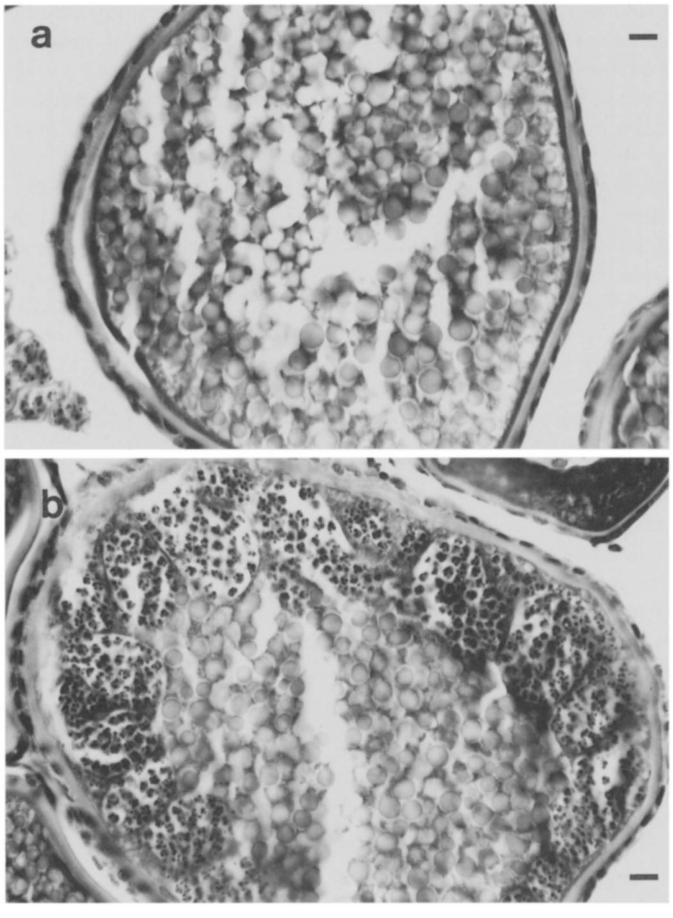

FIGURE 7. Histological preparations of (a) an uninfected mature oocyte and (b) an infected mature oocyte from *Thalassoma bifasciatum.* Plasmodia are situated between the inner boundary of the cell membrane and the yolk granules. Scale bar = 15 μm.

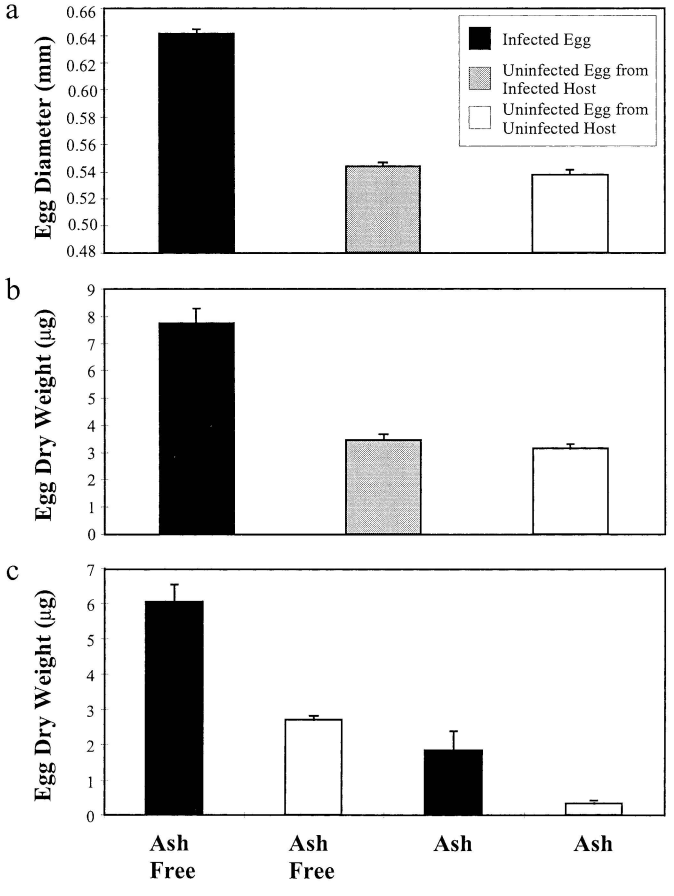

FIGURE 8. Mean differences in (a) diameter, (b) dry weight, and (c) ash and ash-free dry weights between eggs infected with *Kudoa ovivora* spores and uninfected eggs from the ovaries of *Thalassoma bifasciatum* (bars = SE).

TABLE V. Results of a Tukey multiple-comparisons test for differences in *T. bifasciatum* (a) egg diameter (n = number of eggs) and (b) egg dry weight (n = number of egg clutches) among infected eggs and uninfected eggs from both infected and uninfected females.*

	Egg type	Mean egg diameter	n	Comparison	q	$q_{0.05,323,3}$	Conclusion
(a)	Infected (1)	0.641	106	1 vs. 2	44.796	3.314	1 > 2
	Uninfected from infected host (2)	0.544	120	1 vs. 3	45.664	3.314	1 > 3
	Uninfected from uninfected host (3)	0.538	100	2 vs. 3	2.916	3.314	2 = 3
	Egg type	Mean egg dry weight	n	Comparison	q	$q_{0.05,69,3}$	Conclusion
(b)	Infected (1)	7.732	28	1 vs. 2	10.230	3.399	1 > 2
	Uninfected from infected host (2)	3.138	13	1 vs. 3	12.327	3.399	1 > 3
	Uninfected from uninfected host (3)	3.432	31	2 vs. 3	0.665	3.399	2 = 3

* $q = \bar{X}_B - \bar{X}_A/SE$, $SE = \sqrt{s^2/2(1/n_A + 1/n_B)}$, where n_B and n_A = the number of females of each species in the comparison and s^2 is the error mean square of the analysis of variance (ANOVA) of egg diameter or egg dry weight.

capsules. Within this group, there are 2 clusters that are differentiated by spore size: *K. ovivora, K. cascasia, K. funduli,* and *K. leiostomi* are larger than *K. chilkaensis, K. cerebralis,* and *K. sciaenae.* Thus, *K. cascasia, K. funduli,* and *K. leiostomi* are the most taxonomically similar species to *K. ovivora.*

In comparison to our cluster analysis using taxonomic characters, a recently published molecular phylogeny of 4 *Kudoa* species (*K. amamiensis, K. paniformis, K. miniauriculata,* and *Kudoa thyrsites*) found a different pattern of similarity with *K. amamiensis* the most genetically distant species (Hervio et al., 1997). Based on this phylogeny, species tend to cluster more by geographic locality than by spore morphology. Whereas their phylogeny is based on <10% genetic dissimilarity between each species pair, it does suggest a need to reevaluate which taxonomic traits should be used to classify species in this genus.

Mode of transmission

Unlike other myxosporean species, spores of *K. ovivora* are encapsulated within pelagically spawned eggs and not shed directly into seawater. Therefore, transmission of *K. ovivora,* whether fish-to-fish or to an intermediate host, is a function of the dispersal of infected eggs. This is determined primarily by local current patterns and the sinking rate of infected eggs, which are negatively buoyant unlike uninfected eggs that are positively buoyant (S. Swearer and D. Robertson, unpubl. obs.). In San Blas, reef fish populations in areas of reduced current flow have higher levels of infection than populations where spawned eggs are more rapidly carried off the reef. These differences in the level of infection among reefs remain relatively consistent over time (6 yr) (S. Swearer and D. Robertson, unpubl. obs.). This suggests that heavily infected reef fish populations may be chronically exposed to locally spawned infected eggs, therefore facilitating the maintenance of the infection within the population.

The preliminary results of our feeding experiment suggest that infections within a population can occur by fish-to-fish transmission through the ingestion of infected pelagically spawned eggs. *Thalassoma bifasciatum* are known to cannibalize conspecific eggs (D. Robertson, unpubl. obs.) and we have witnessed individuals feeding on conspicuously colored infected eggs. Because *K. ovivora* infections appear to be transmitted directly, alterations of egg size, color, and buoyancy may prove to be parasite adaptations that increase the probability of trophic transfer (Lafferty, 1992). The observation that larger and, therefore, most likely older females, have a higher prevalence of infection than smaller, younger females is consistent with a trophic transfer model because older individuals have a longer exposure history to infected eggs and larger fish with greater gut capacities may eat more infected eggs. However, we cannot exclude the possibility that *K. ovivora* spores are transmitted to another host resident on coral reefs. Unfortunately, *T. bifasciatum* females were not easily kept in captivity. Much of the mortality experienced during the experiment resulted from intraspecific aggression. This source of stress likely caused many of the surviving females, especially smaller subordinate ones, to shut down reproduction, making it difficult to assess whether these individuals were infected with *K. ovivora.* Almost all the fish with active ovaries were 1 of the 2 largest females in each aquarium (10 out of 11). Larger sample sizes of unequivocally parasite-free fish are needed to determine conclusively whether *K. ovivora* is trophically transferred from one fish host to another by the ingestion of infected eggs.

Life history consequences of infection

Sporogenesis in *K. ovivora* occurs within developing oocytes in the ovaries of the host fish. The timing of sporogenesis appears to coincide with the onset of vitellogenesis, when the majority of food resources needed for embryonic development are transferred into the egg cell. The initial infective stages (trophozoites containing the spore-producing generative cells) in the genus *Kudoa* are quite small relative to the oocyte (Lom and Dyková, 1988, 1992). Therefore, differences in egg dry weights between infected eggs and uninfected eggs are predominantly a result of increased resource allocation to infected eggs because we would predict no weight difference (or perhaps a drop in weight) if normal egg resource levels were simply converted into spores. We determined that *K. ovivora* increases both the nutrient (organic) and inorganic content of the egg.

Thus, infected females suffer both an energetic cost through the production and release of infected eggs as well as a reduction in reproductive success through a decrease in the number of viable offspring. These fitness costs are apparently permanent because infected females remain infected over time even

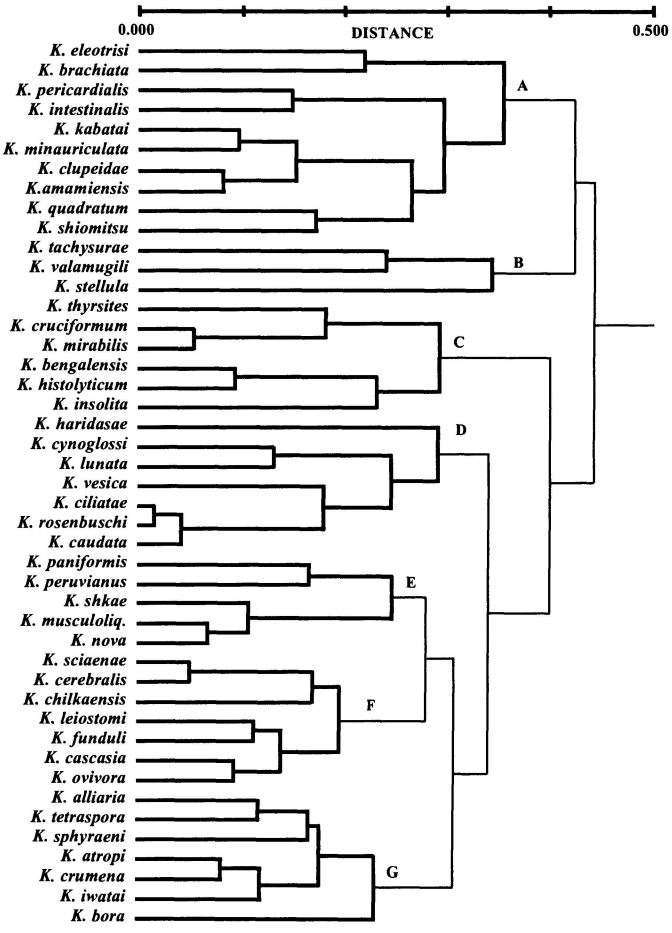

FIGURE 9. Tree dendrogram of the average linkage cluster analysis of all currently identified *Kudoa* species (distance = degree of dissimilarity; 0 = complete similarity, 1 = complete dissimilarity). Labeled clusters are defined as follows: A, small quadrate spores with both lateral and apical valve extensions and equal-sized polar capsules; B, small spores with only lateral valve extensions and unequal ovate polar capsules; C, large stellate spores with only lateral valve extensions and nonpyriform polar capsules; D, moderate-sized stellate spores with equal-size pyriform polar capsules; E, moderate-sized spores lacking both lateral and apical valve extensions with equal-sized ovate polar capsules; F, moderate-sized quadrate spores with only apical valve extensions and equal-sized pyriform polar capsules; G, large quadrate spores lacking lateral valve extensions with equal-sized elongate polar capsules.

with the continual release of infected eggs (S. Swearer and D. Robertson, unpubl. obs.). Because we did not observe any presporogenic stages of *K. ovivora* within infected ovaries, this suggests that *K. ovivora* may have a proliferative or extrasporogenic stage occurring outside the ovary which produces the sporogenic stages within oocytes (Lom and Dyková, 1992).

There are 2 additional aspects of the reproductive biology of the host group of fishes that suggest other potential fitness costs associated with *K. ovivora* infections. Female bluehead wrasse in San Blas spawn, on average, at least 2 out of every 3 days (Schultz and Warner, 1989; Robertson et al., 1998) and spawning occurs throughout much of the year (Warner et al., 1975; Robertson et al., 1998). If transmission of *K. ovivora* is facilitated by the dispersal of pelagically spawned eggs, selection would favor the parasite increasing the amount of energy the host allocates to reproduction, both in terms of spawning frequency and the number of eggs released during spawning. If *K. ovivora* can regulate the energy allocation decisions of the host when food resources are limiting, we would expect infected females to have slower growth rates compared to uninfected females as a cost of maintaining high levels of reproduction.

Kudoa ovivora may also impact its host by modifying its reproductive allocation strategy. All species found to be susceptible to infection by *K. ovivora* are sequential hermaphrodites (Robertson and Warner, 1978; Warner and Robertson, 1978). Under certain social conditions, mature females will change sex and become males (Warner et al., 1975; Warner and Swearer, 1991). Because males of these species do not appear to be susceptible to infection by *K. ovivora,* at least not in terms of sporogenesis in the gonad or any other tissue, infected females could potentially rid themselves of the infection by changing sex. Conversely, in order to maintain the infection, *K. ovivora* should prevent sex change of the host. These potential energetic and sex allocation costs associated with *K. ovivora* infections warrant further study.

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APPENDIX. Part I. Summary of the taxonomic characteristics of the species *Kudoa alliaria* through *Kudoa ovivora*

Species name	Host(s)	Site of infection	Locality	Number of spores/ trophozoite
Kudoa alliaria	*Micromesistius australis, Notothenia ramzay, Notothenia conina, Macruronus magellanicus*	Musculature	SW Atlantic Ocean	—
Kudoa amamiensis	*Abudefduf sexfasciatus, Abudefduf vagiensis, Chromis isharai, Chromis notatus, Chrysiptera assimilis, Seriola quinqueradiata*	Musculature	Japan	Polysporous
Kudoa atropi	*Atropis atropis*	Gills	West Bengal, India	Polysporous
Kudoa bengalensis	*Tachysurus platystomus*	Skeletal musculature	West Bengal, India	—
Kudoa bora	*Mugil japonica*	Musculature	Taiwan	Polysporous
Kudoa brachiata	*Leiostomus xanthurus*	Gills	Texas, U.S.A.	—
Kudoa cascasia	*Sicamugil cascasia*	Intestinal mesentery	West Bengal, India	Polysporous
Kudoa caudata	*Scomber japonicus*	Musculature	SE Pacific Ocean	—
Kudoa cerebralis	*Morone saxatilis*	Brain	Chesapeake Bay, U.S.A.	Polysporous
Kudoa chilkaensis	*Strongylura strongylura*	Musculature	India	—
Kudoa ciliatae	*Sillago ciliata*	Intestinal musculature	New South Wales, Australia	Polysporous
Kudoa clupeidae	*Clupea harengus, Pomolobus pseudoharengus, Pomolobus aestivalis*	Musculature	Massachusetts, U.S.A.	Polysporous
Kudoa clupeidae	*Brevoortia tyrannus*	Musculature	North Carolina, U.S.A.	Polysporous
Kudoa cruciformum	*Lateolabrax japonicus*	Musculature	Japan	—
Kudoa crumena	*Scomberomorus maculatus*	Musculature	South Florida, U.S.A.	Polysporous
Kudoa cynoglossi	*Cynoglossus senegalensis*	Skeletal musculature	East Coast of Nigeria	Polysporous
Kudoa eleotrisi	*Eleotris kribensis*	Gills	Benin, West Africa	Polysporous
Kudoa funduli	*Fundulis heteroclitus, Fundulus majalis*	Musculature, fins	Massachusetts, U.S.A.	Polysporous
Kudoa funduli	*Fundulus heteroclitus*	Musculature, fins	New Jersey, U.S.A.	Polysporous
Kudoa haridasae	*Mugil persina*	Gallbladder	West Bengal, India	—
Kudoa histolyticum	*Scomber scombrus*	Musculature	SW France	Polysporous
Kudoa insolita	*Seriola dumerili*	Musculature	Atlantic Ocean	—
Kudoa intestinalis	*Mugil cephalus*	Intestinal musculature	Japan	Polysporous
Kudoa iwatai	*Pagrus major, Oplegnathus punctatus*	Musculature	Japan	Polysporous
Kudoa kabatai	*Zeugopterus punctatus*	Musculature	North Sea	Polysporous
Kudoa leiostomi	*Leiostomus xanthurus*	Trunk musculature	Gulf of Mexico	Polysporous
Kudoa lunata	*Arnoglossus imperialis, Arnoglossus laterna, Arnoglossus thori*	Skeletal musculature	Mediterranean	Polysporous
Kudoa miniauriculata	*Sebastes paucispinis*	Somatic musculature	California, U.S.A.	Polysporous
Kudoa mirabilis	*Trichiurus haumela*	Musculature	Yemen	Polysporous
Kudoa musculoliquefaciens	*Xiphias gladus*	Musculature	Japan	Polysporous
Kudoa nova	*Pagellus acarne* (see ref. for complete species list)	Musculature	Atlantic Ocean, Mediterranean, Black Sea, and Sea of Azov	Polysporous
Kudoa ovivora	***Thalassoma bifasciatum, Halichoeres bivittatus, Halichoeres garnoti, Halichoeres poeyi, Sparisoma aurofrenatum, Sparisoma radians, Sparisoma rubripinne***	**Ovary**	**Caribbean**	**Polysporous**

APPENDIX. Part I. Extended.

Spore shape in apical view	Mean spore length (range)	Mean spore width (range)*	Mean spore thickness (range)*	Polar capsule shape	Mean polar capsule length (range)*
Quadrate	— (7.0–8.0)	— (9.0–10.0)	— (8.0–9.0)	—	2.4 (—)
Quadrate	— (4.5–5.0)	— (5.0–6.0)	— (5.0–6.0)	Pyriform	— (1.5–2.0)
Quadrate	10.0 (9.0–11.0)	10.0 (9.0–11.0)	9.0 (8.0–9.0)	Pyriform	3.3 (3.0–3.6)
Stellate	7.9 (7.0–8.5)	8.4 (7.0–11.0)	—	Elongate	3.8 (3.0–4.8)
Ovate	— (8–8.5)	— (11.0–12.0)	— (11.0–12.0)	Elongate	5.5 (—)
Quadrate	4.2 (3.9–4.9)	4.7 (4.4–4.9)	4.7 (4.4–4.9)	Pyriform	1.5 (—)
Quadrate	6.6 (6.0–8.0)	8.2 (7.0–9.0)	7.6 (7.0–8.0)	Pyriform	3.1 (2.5–3.5)
Quadrate	— (5.3–6.7)	— (8.0–8.6)	6.7 (—)	Pyriform	— (2.0–2.7)
Quadrate	5.5 (4.8–5.8)	7.0 (4.8–8.6)	6.4 (5.8–7.2)	Pyriform	3.7 (2.6–4.7)
Quadrate	5.5 (—)	7.2 (—)	5.8 (—)	Pyriform	3.5 (—)
Quadrate	5.5 (5.0–6.3)	8.9 (8.2–9.7)	6.5 (6.0–7.0)	Pyriform	2.4 (1.9–2.7)
Quadrate	5.0 (—)	—	7.0 (—)	Pyriform	2.0 (—)
Quadrate	5.1 (—)	—	6.4 (—)	Pyriform	1.5 (—)
Stellate	7.0 (7.0–9.1)	L: 16.0 (14.0–18.2) S: 15.1 (13.6–16.8)	L: 12.6 (11.2–15.4) S: 9.7 (8.4–11.2)	Ovate	L: 6.3 (5.6–7.8) S: 4.0 (2.8–4.9)
Quadrate	7.5 (6.8–8.2)	9.9 (9.3–10.4)	9.0 (8.2–9.7)	Pyriform	4.0 (3.2–4.6)
Stellate	6.2 (5.8–6.5)	14.1 (13.8–14.4)	10.2 (10.0–10.6)	Pyriform	— (2.9–3.2)
Quadrate	—	—	6.5 (5.5–8.0)	Pyriform	1.6 (—)
Quadrate	7.5 (—)	6.0 (—)	6.0 (—)	Pyriform	—
Quadrate	8.4 (—)	6.7 (—)	6.7 (—)	Pyriform	3.3 (—)
Stellate	5.0 (4.0–5.5)	10.1 (9.0–11.0)	—	Ovate	2.8 (2.0–3.0)
Stellate	— (7.0–9.0)	— (12.0–15.0)	—	Elongate	— (3.0–6.0)
Quadrate	— (4.2–5.3)	— (6.4–7.5)	— (5.3–6.5)	—	— (3.2–3.7)
Quadrate	3.4 (3.0–3.5)	6.5 (6.3–7.0)	6.1 (5.8–6.5)	Ovate	1.5 (1.3–1.5)
Quadrate	7.2 (6.7–8.0)	10.1 (9.7–10.7)	9.1 (8.8–9.6)	Pyriform	4.0 (3.8–4.5)
Stellate	— (4.0–5.0)	— (5.0–7.7)	—	—	— (1.5–2.0)
Quadrate	6.8 (—)	9.1 (8.0–9.8)	6.5 (5.8–7.0)	Pyriform	3.3 (—)
Stellate	5.3 (4.5–6.2)	10.0 (9.0–11.4)	—	Pyriform	2.5 (2.0–3.0)
Stellate	5.4 (5.0–5.9)	7.9 (7.0–8.5)	—	Pyriform	2.2 (1.8–2.3)
Stellate	— (6.6–8.8)	— (10.3–10.4)	— (8.1–12.0)	Ovate	L: — (5.9–7.7) S: — (2.9–4.4)
Quadrate	6.2 (5.3–7.3)	8.4 (7.4–9.9)	7.9 (7.0–9.0)	Ovate	2.1 (1.7–2.8)
Quadrate	— (5.3–6.5)	— (8.5–9.8)	— (7.5–8.0)	Ovate	— (2.7–3.2)
Quadrate	**6.5 (5.0–7.5)**	**7.7 (6.7–8.3)**	**6.9 (5.8–7.7)**	**Pyriform**	**2.1 (1.7–2.5)**

* L = large, M = medium, S = small for species with multiple spore or polar capsule types. All measurements are in μm.

APPENDIX. Part I. Extended.

Species name	Mean polar capsule breadth (range)*	Apical valve extensions	Lateral valve extensions	Reference(s)
Kudoa alliaria	1.8 (—)	—	Absent	Kovaleva et al. (1979)
Kudoa amamiensis	— (1.0–1.2)	Present	Present—papillae	Egusa and Nakajima (1980)
Kudoa atropi	1.7 (1.6–1.8)	—	Absent	Sandeep et al. (1986)
Kudoa bengalensis	2.0 (1.8–2.0)	Absent	Present	Sarkar and Mazumder (1983)
Kudoa bora	1.8 (—)	Present	Absent	Fujita (1930)
Kudoa brachiata	1.0 (—)	—	Present	Joy (1972)
Kudoa cascasia	1.6 (1.2–2.0)	Present	Absent	Sarkar and Chaudry (1996)
Kudoa caudata	— (1.6–2.0)	Absent	Present—filaments	Kovaleva and Gaevskaya (1983)
Kudoa cerebralis	1.5 (1.0–1.8)	Absent	Absent	Paperna and Zwerner (1974)
Kudoa chilkaensis	— (1.0–1.5)	Present	Absent	Tripathi (1951)
Kudoa ciliatae	1.4 (1.2–1.9)	Absent	Present	Lom et al. (1992)
Kudoa clupeidae	1.0 (—)	—	—	Hahn (1917)
Kudoa clupeidae	1.0 (—)	Present	Present	Meglitsch (1947)
Kudoa cruciformum	L: 3.1 (2.5–3.6) S: 2.1 (1.7–2.8)	Absent	Present	Matsumoto (1954)
Kudoa crumena	2.5 (2.1–2.9)	Absent	Absent	Iversen and Van Meter (1967)
Kudoa cynoglossi	— (2.0–2.5)	Present—2.1	Present—2.0	Obiekezie and Lick (1994)
Kudoa eleotrisi	—	—	Absent	Siau (1971)
Kudoa funduli	—	Present	Absent	Hahn (1915)
Kudoa funduli	1.5 (—)	Present	Absent	Meglitsch (1948)
Kudoa haridasae	1.1 (1.0–1.2)	Absent	Present—lateral inflations	Sarkar and Ghosh (1991)
Kudoa histolyticum	3.0 (—)	Absent	Present	Pérard (1928)
Kudoa insolita	2.0 (—)	—	—	Kovaleva et al. (1979)
Kudoa intestinalis	1.2 (1.0–1.5)	Present	Absent	Maeno et al. (1993)
Kudoa iwatai	2.2 (2.0–2.4)	Present	Absent	Egusa and Shiomitsu (1983)
Kudoa kabatai	—	Present	Present	Kovaleva et al. (1979)
Kudoa leiostomi	1.7 (—)	Present—apical thickenings	Absent	Dyková et al. (1994)
Kudoa lunata	1.5 (1.4–1.7)	Present	Present—0.7	Lom et al. (1983)
Kudoa miniauriculata	—	Present—very small	Present	Whitaker et al. (1996)
Kudoa mirabilis	L: — (4.7–5.2) S: — (1.6–2.2)	—	Present	Naidenova and Gaevskaya (1991)
Kudoa musculoliquefaciens	2.0 (1.7–2.5)	Absent	Absent	Matsumoto (1954)
Kudoa nova	2.0 (—)	—	Absent	Kovaleva et al. (1979)
Kudoa ovivora	**1.5 (1.3–1.7)**	**Present**	**Absent**	**This paper**

* L = large, M = medium, S = small for species with multiple spore or polar capsule types. All measurements are in μm.

APPENDIX. Part II. Summary of the taxonomic characteristics of the species *Kudoa paniformis* through *Kudoa vesica*

Species name	Host(s)	Site of infection	Locality	Number of spores/ trophozoite
Kudoa paniformis	*Merluccius productus*	Musculature	British Columbia	Polysporous
Kudoa pericardialis	*Seriola quinqueradiata*	Pericardial cavity	Japan	Polysporous
Kudoa peruvianus	*Merluccius gayii*	Musculature	Peru	Polysporous
Kudoa quadratum	*Callionymus lyra, Coris julis, Entelurus olquerus, Julis vulgaris, Myoxcephalus scorpius, Nerophis aequoris, Syngnathus acus, Trachurus trachurus*	Musculature	Atlantic Ocean, Mediterranean and White Sea	—
Kudoa rosenbuschi	*Merluccius gayii*	Musculature	Argentina	Polysporous
Kudoa sciaenae	*Sciaenae deliciosa, Sciaenae fasciata, Stellifer minor, Paralonchurus peruanus*	Musculature	Peru	—
Kudoa shiomitsu	*Takifugu rubripes*	Pericardial cavity, heart	Japan	—
Kudoa shkae	*Arius felis*	Trunk musculature	Gulf of Mexico	Polysporous
Kudoa sphyraeni	*Sphyraena jello*	Gut musculature	India	Polysporous
Kudoa stellula	*Atherina hepsetus*	Kidney	Black Sea	—
Kudoa tetraspora	*Mugil cephalus*	Brain, optic lobes	India	Polysporous
Kudoa thyrsites	*Thyrsites atun*	Musculature	South Africa	Monosporous
Kudoa thyrsites	*Merluccius productus*	Musculature	British Columbia	Monosporous
Kudoa thyrsites	*Coryphaena hippurus*	Skeletal and cardiac musculature, pericardium, liver	SW Australia	Monosporous
Kudoa tachysurae	*Tachysurus tenuispinis*	Gallbladder	West Bengal, India	—
Kudoa valamugili	*Valamugil cunnesius*	Intestinal musculature	India	Polysporous
Kudoa vesica	*Pseudoicichthys australis*	Urinary vesicle	Antarctica	—
Kudoa sp.	*Sparus aurata*	Kidney	France	Disporous
Kudoa sp.	*Sparus aurata*	Mesentery, peritoneum	Israel	Disporous
Kudoa sp.	*Morone americana*	Musculature, liver, spleen, peripancreatic tissue	Chesapeake Bay, U.S.A.	Polysporous
Kudoa sp.	*Hemiscyllium ocellatum*	Musculature	NE Australia	Polysporous

APPENDIX. Part II. Extended.

Species name	Spore shape in apical view	Mean spore length (range)	Mean spore width (range)*	Mean spore thickness (range)*	Polar capsule shape
Kudoa paniformis	Stellate	5.0 (4.5–6.0)	6.7 (6.0–7.0)	5.9 (5.0–6.5)	Pyriform
Kudoa pericardialis	Quadrate	— (4.0–4.2)	— (6.0–7.0)	— (4.5–5.0)	Elongate
Kudoa peruvianus	Ovate	— (4.7–5.1)	— (5.6–6.5)	—	Ovate
Kudoa quadratum	Quadrate	— (6–7)	—	5.0 (—)	—
Kudoa rosenbuschi	Quadrate	—	—	7.0 (—)	Pyriform
Kudoa sciaenae	Quadrate	5.3 (4.8–6.4)	—	6.4 (—)	Pyriform
Kudoa shiomitsu	Quadrate	6.2 (5.6–6.8)	9.4 (8.6–9.8)	7.2 (6.7–7.5)	Elongate
Kudoa shkae	Ovate	6.2 (6.1–6.2)	7.5 (7.0–8.1)	7.5 (7.0–8.1)	Ovate
Kudoa sphyraeni	Quadrate	9.4 (9.0–10.2)	9.8 (9.5–10.5)	9.8 (9.5–10.5)	Elongate
Kudoa stellula	Stellate	—	— (5.0–6.9)	— (3.7–4.7)	Ovate
Kudoa tetraspora	Quadrate	—	9.0 (—)	9.0 (—)	Elongate
Kudoa thyrsites	Stellate	8.0 (—)	12.0 (—)	—	Ovate
Kudoa thyrsites	Stellate	7.1 (6.0–8.0)	16.7 (14.0–19.0)	L: 12.7 (10.0–14.0) S: 8.0 (6.0–10.0)	Ovate
Kudoa thyrsites	Stellate	— (7.3–8.2)	14.0 (12.3–16.3)	L: 10.3 (9.3–11.3) S: 7.8 (7.3–8.5)	Ovate
Kudoa tachysurae	Quadrate	4.9 (4.5–6.0)	7.8 (7.0–9.0)	5.5 (5.0–6.5)	Pyriform
Kudoa valamugili	Quadrate	5.6 (5.2–6.6)	5.3 (5.0–5.4)	4.7 (4.3–5.6)	Pyriform
Kudoa vesica	Stellate	— (5.3–6.7)	— (8.0–10.6)	— (8.0–9.9)	Pyriform
Kudoa sp.	Quadrate	13.6 (—)	— (15.3–17.0)	— (13.6–15.3)	Pyriform
Kudoa sp.	Quadrate	— (6.4–8.0)	— (6.4–8.8)	— (6.4–8.8)	Pyriform
Kudoa sp.	—	4.0 (3.5–4.5)	6.6 (5.5–8.0)	5.7 (5.0–6.5)	Ovate
Kudoa sp.	Quadrate	— (5.5–7.0)	—	—	Pyriform

* L = large, M = medium, S = small for species with multiple spore or polar capsule types. All measurements are in μm.

APPENDIX. Part II. Extended.

Mean polar capsule length (range)*	Mean polar capsule breadth (range)*	Apical valve extensions	Lateral valve extensions	Reference(s)
21(2.0–2.5)	1.7 (1.5–2.0)	Absent	Absent	Kabata and Whitaker (1981)
—(2.4–3.0)	— (1.0–1.5)	Present—polar lids	Absent	Nakajima and Egusa (1978)
—(2.2–2.7)	— (1.3–1.8)	Absent	Absent	Salas (1972)
—	—	Present	Present	Thélohan (1895); Kovaleva et al. (1979); Lom and Dyková (1992)
2.5 (—)	—	—	Present	Gelormini (1943)
3.2 (—)	1.6 (—)	Absent	Absent	Teran et al. (1990)
2.8 (2.5–3.0)	1.3 (1.0–1.4)	Present	Present	Egusa and Shiomitsu (1983)
2.5 (—)	2.0 (—)	Absent	Absent	Dyková et al. (1994)
3.6(—)	— (1.0–1.6)	Absent	Absent	Narasimhamurti and Kalavati (1979b)
L: —(2.0—2.2) M: — (1.7–2.0) S: — (1.5–1.9)	L: — (1.5–1.6) M: — (1.3–1.5) S: — (0.9–1.4)	—	Present	Jurakhno (1991)
— (3.4–4.0)	— (1.5–1.8)	Absent	Absent	Narasimhamurti and Kalavati (1979a)
L: 3.0(—) M: 2.3(—) S: 1.5(—)	L: 2.0 (—) M: 1.5 (—) S: 1.0 (—)	Absent	Present	Gilchrist (1924)
L: 5.4 (4.9–5.9) S: 1.0 (2.9–4.9)	L: 3.3 (2.8–3.9) S: 2.4 (2.0–2.9)	Absent	Present	Kabata and Whitaker (1981)
L: 6.3 (5.8–6.9) M: 5.1 (4.2–5.5) S: 4.3 (3.8–4.8)	L: 2.9 (2.7–3.2) M: 2.3 (2.2–2.6) S: 1.9 (1.8–2.3)	Absent	Present	Langdon (1991)
L: 3.3 (3.0–4.0) S: 1.5 (1.0–1.5)	L: 2.5 (2.0–3.0) S: 1.4 (1.0–1.5)	Absent	Present	Sarkar and Mazumder (1983)
L: 3.2 (3.0–3.8) S: 2.4 (2.0–3.2)	L: 1.8 (1.6–2.0) S: 1.4 (1.2–1.6)	Absent	Absent	Kalavati and Anuradha (1993)
—(2.0–2.7)	1.3 (—)	Absent	Present	Kovaleva and Gaevskaya (1984)
6.8 (—)	—	—	Absent	Paperna (1982)
—(3.2–4.0)	—	—	Absent	Paperna (1982)
L: 4.0 (3.5–4.5) S: 2.6 (2.–03.0)	L: 2.4 (2.0–3.0) S: 1.0 (1.0–1.3)	Absent	Absent	Bunton and Poynton (1991)
—	L: 2.4 (—)	—	—	Heupel and Bennett (1996)

* L = large, M = medium, S = small for species with multiple spore or polar capsule types. All measurements are in μm.