Synopsis of myxosporean species (Cnidaria: Myxozoa) parasitizing fishes from Vietnam

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Abstract

This paper provides an update checklist of species-level identified myxosporean species from marine and freshwater fishes in Vietnam. The list includes 51 nominal myxosporean species (38 marine and 13 freshwater) belonging to 9 genera: *Myxobolus* (26 species); *Kudoa* (6 species); *Henneguya* (6 species); *Thelohanellus* (5 species); *Unicapsula* (2 species); *Ceratomyxa* (2 species), *Zschokkella* (2 species); *Auerbachia* (1 species), and *Meglitschia* (1 species). For each parasite species, information on morphological characteristics of myxospore, fish hosts, infection sites, and collection locality in Vietnam along with GenBank accession number of nucleotide sequence data and the line drawings were provided. In addition, taxonomic status of several species was discussed and *Myxobolus eszterbaueri* nom. nov. is proposed as a junior homonym for *Myxobolus hakyi* Baska, Voronin, Eszterbauer, Müller, Marton & Molnár 2009.

Introduction

Myxosporeans (Cnidaria: Myxozoa) are common parasites of fish. The majority of these species parasitize various fishes from fresh, marine and brackish waters all over the world, while few species are reported from amphibians, reptiles, birds, and mammals (Eiras et al., 2005; Lom & Dyková 2006; Prunescu et al., 2007; Bartholomew et al. 2008; Hartigan et al. 2016). To date, more than 2,600 myxosporean species spanning 2 orders, 17 families and 64 genera have been described (Fiala et al., 2015; Zatti et al., 2015; Lisnerová et al., 2022). Generally, pathological affection of myxosporean species to their fish hosts is mild. However, some species cause severe disease, mortality, value loss of fishery products, or even food poisoning to humans (Bartholomew & Reno, 2002; Liu et al., 2019; Holzer et al., 2021). Therefore, myxospores are considered important pathogens in both wild and farmed fishes.

In Vietnam, studies of myxosporean parasites in fish began in 1971 with the first report by Ky (1971) in which seventeen species, including twelve new species, in freshwater fish from Northern Vietnam were described. Later in 2006, when Arthur and Te (2006) listed 33 myxosporean species from freshwater fishes from various locations of Vietnam, including five undescribed species. Recently, research on mxyosporean diversity in Vietnam has been expanded with more thorough sampling and utilization of molecular analyses and detailed morphological descriptions. As a result, eleven myxosporean species, including 4 new species, have been added to Vietnamese myxosporean fauna over the last 8 years (Tomochi et al., 2014; Chinh, 2021; Chinh et al., 2021; Chinh et al., 2022a, 2022b; Yurakhno et al., 2022).

To bring together the less accessible earlier reports and the more recent research advances, this synopsis aims to systematically summarize and provide up-to-date information on myxosporeans parasitizing marine and freshwater fishes from Vietnam.

Materials And Methods

The information used in this study was obtained from books and articles published in international and local scientific journals up to December 2022. Non-peer-reviewed reports in conference abstracts and university theses were not included. Unidentified species reported with limited or ambiguous information were excluded. The scientific names for myxosporeans and fish hosts follow the World Register of Marine Species (https://www.marinespecies.org/) and FishBase (https://www.fishbase.se/search.php), respectively. The DNA sequence data of one species, *Unicapsula andersenae*, infecting in the muscle of Boeseman croaker *Boesemania microlepis* collected in Nha Trang (Khanh Hoa province) in January 2023, was obtained as similar method to these used in our previous study on *Henneguya lata* species (Chinh et al., 2021) with designed primer pair UniF (5'-CAGCCATGGATAACTGTGG-3') and UniR (5'-GATGACTCGCGCTTACGAG-3').

Line drawings of all 51 species were redrawn from their original illustrations or micrographs using Adobe Illustrator CS2 software (Adobe Systems Inc., San Jose, California). In addition, spore dimensions, general myxospore morphology, GenBank accession numbers of ribosomal DNA sequence(s) if available, infection sites, Vietnamese fish hosts, habitats, and collection localities were summarized (Table 1). Species within each genus are listed alphabetically. All measurements are in micrometers (µm).

Table 1
List of the myxosporean specie and their host, features and geographical localities infecting Vietnamese fishes. M: Marine; FW: Freshwater; CA: caudal exten
Polar capsule. ▲: Data was provided in this study.

Parasite	Host	Locality	Habitat	Infection site	Vegetative stage	Spore	GenBank	Polar capsule	Polar filament	F
Family Myxidiidae										
Genus *Zschokkella* Auerbach, 1910										
Zschokkella donetzae Ky, 1971	*Hypophthalmichthys harmandi* Sauvage, 1884	Bac Giang, Bac Ninh	FW	Gall bladder		Elongated oval; 14.4–17.1 (length) × 5.4–6.3 (width) × 5–6 (thickness); Fig. 2		Two PCs, spherical, equal; 3.6–4.5 × 3.2–3.6		K
Zschokkella orientalis Konovalov & Schulman, 1966	*Trichopodus trichopterus* (Pallas, 1770)	Mekong river delta	FW	Gall bladder		Oval-shaped; 10.4–11.2 (length) × 4.8 (width) × 3.2–4.0 (thickness); Fig. 3		Two PCs, spherical, equal; 3.2 × 2.4–3.2	3–4 turns	K 2
Family Ceratomyxidae										
Genus *Ceratomyxa* Thélohan, 1892										
Ceratomyxa binhthuanensis Chinh, Ha, Doanh, Violetta, Yoshinaga, Shirakashi, Hallett & Whipps, 2022	*Epinephelus fasciatus* (Forsskål, 1755)	Binh Thuan	M	Gall bladder	Not observed	Elongate and slightly crescent-shaped; Posterior angle 153.7° (148.9°–166.0°), 12.2 (10.8–16.0) (thickness) × 5.8 (4.8–6.9) (length); Fig. 4	MZ504160	Two PCs, spherical, equal; 2.6 (2.3–2.9) µm in diameter		C a
Ceratomyxa tienensis Ky & Te, 2007	*Pangasianodon hypophthalmus* (Sauvage, 1878)	Dong Thap	FW	Gall bladder		Elongated; 4.5–5.0 (thickness) × 8.4–9.0 (length). Figure 5		Two PCs, spherical, equal; 2.2–2.5 µm in diameter		K 2
Genus *Meglitschia* Kovaljova, 1988										
Meglitschia insolita (Meglitsch, 1960) Kovaljova, 1988	*Epinephelus coioides* (Hamilton, 1822)	Khanh Hoa	M	Gall bladder		V-shaped, dimensions not given; Fig. 6		Two PCs, spherical, equal, dimensions not given		V 2
Family Coccomyxidae										
Genus *Auerbachia* Meglitsch, 1960										
Auerbachia chakravartyi Narasimhamurti, Kalavati, Anuradha & Padma, 1990	*Megalaspis cordyla* (Linnaeus, 1758)	Quang Bình, Khanh Hoa	M	Gall bladder		Club-shaped; 17.5 (15.8–20.7) (total length) × 7.7 (7.1–8.3) (width) × 8.8 (7.6–10.4) (caudal extension length); Fig. 7	MZ505546	One PC, elliptical; 8.5 (5.8–9.6) × 3.9 (3.5–4.2) (width)		C 2
Family Myxobolidae										
Genus *Myxobolus* Bütschli, 1882										

Parasite	Host	Locality	Habitat	Infection site	Vegetative stage	Spore	GenBank	Polar capsule	Polar filament	F
Myxobolus achmerovi Schulman, 1966	*Cyprinus carpio* Linnaeus, 1758	Bac Ninh, Bac Giang, Ha Noi, Ha Nam, Nam Dinh, Ninh Binh, Bac Can	FW	Skin, gill, intestine	Circle-shaped, 0.26–1 mm in diameter	Oval-shaped; 10–13.5 (length) × 9–11.7 (width) × 8.6 (thickness); Fig. 8		Two PCs, pyriform-shaped, equal; 4.5–5.4 (length) × 2.7–3.6 (width)	57.6–68.4 μm in length	K 2
Myxobolus anisocapsularis Schulman, 1962	*Cyprinus carpio* Linnaeus, 1758	Bac Ninh, Bac Giang, Ha Noi	FW	Gill	Oval or circle-shaped, up to 2 in diameter	Pear-shaped; 12.6–14,5 (length) × 7–7.5 (width) × 5.5 (thickness); Fig. 9		Two PCs, pyriform-shaped, unequal; The larger 7.2–8.1 (length) × 2.7–3.6 (width). The smaller 2.7–4.0 (length) × 1 (width)		K 2
Myxobolus artus Achmerov, 1960	*Cyprinus carpio* Linnaeus, 1758	Hanoi, Bac Ninh, Bac Giang, Ha Nam, Nam Dinh, Ninh Binh	FW	Skin, gill, intestine	Not observed	Oval-shaped; 6.6–8.2 (length) × 9.9–11.5 (width) × 8.2 (thickness); Fig. 10		Two PCs, pyriform-shaped, equal; 4.9 (length) × 3.3 (width)		K 2
Myxobolus cheisini Schulman, 1962	*Leptobarbus hoevenii* (Bleeker, 1851)	Mekong river delta	FW	Skin, Gill	Oval-shaped, 0.45–0.55mm diameter	Pear-shaped; 13.2–14 (length) × 7.6 (width) × 6.2 (thickness); Fig. 11		Two PCs, pyriform-shaped, equal; 7.6 (length) × 3.1 (width)	8 turns, 17–22 μm in length	K 2
Myxobolus clarii Chakravarty, 1943	*Clarias batrachus* (Linnaeus, 1758); *Clarias macrocephalus* Günther, 1864	Mekong river delta	FW	Kidney, liver, abdominal cavity	Oval-shaped	Pear-shaped; 14–15.5 (length) ×10.9–12.4 (width) × 9.3 (thickness); Fig. 12		Two PCs, pyriform-shaped, equal; 7.6–9.3 (length) × 4.7–5.4 (width)		K 2
Myxobolus cyprini Doflein, 1898	*Cyprinus carpio* Linnaeus, 1758	Quang Binh, Quang Tri, Thua Thien Hue	FW	Skin	Spherical or oval-shaped; 1 mm in diameter	Oval-shaped; 10–16 (length) × 8–12 (width) × 5.4–6 (thickness); Fig. 13		Two PCs, pyriform-shaped, equal; 5.2–7 (length)		K 2
Myxobolus cyprinicola Reuss, 1906	*Cyprinus carpio* Linnaeus, 1758	Bac Ninh, Bac Giang, Ha Noi	FW	Gill	Oval-shaped, 0.5 x 0.3 mm	Oval-shaped; 9–13.5 (length) × 7–10 (width) × 5.6–6.5 (thickness); Fig. 14		Two PCs, pyriform-shaped, equal; 4.2–5.2 (length) × 2.5–3 (width)	40 μm in length	K 2
Myxobolus discapsularis Ky, 1971	*Hypophthalmichthys harmandi* Sauvage, 1884	Bac Giang, Bac Ninh	FW	Gall bladder		Oval-shaped; 12.6–13.5 (length) × 9–10.8 (width); Fig. 15		Two PCs, pyriform-shaped, unequal; The bigger 7.2 (length) × 3.6 (width). The smaller 2.7–3.6 (length) × 1.8 (width)		K

Parasite	Host	Locality	Habitat	Infection site	Vegetative stage	Spore	GenBank	Polar capsule	Polar filament	F
Myxobolus divergens Ky, 1971	*Aristichthys nobilis* (Richardson, 1845)	Ha Noi, Bac Ninh, Bac Giang	FW	Gill, Skin, liver, kidney, spleen	Oval-shaped	Pear-shaped; 14.4–16.2 (length) × 9–10 (width); Fig. 16		Two PCs, pyriform-shaped, equal; 5.4 (length) × 3.6 (width)		K
Myxobolus ellipticus Ky, 1971	*Hypophthalmichthys harmandi* Sauvage, 1884	Ha Noi	FW	Gill	Oval-shaped	Pear-shaped; 2.6–14.4 (length) ×9–10.8 (width); Fig. 17		Two PCs, pyriform-shaped, equal; 5.4–7.2 (length) × 3.6 (width)	5 turns	K
Myxobolus exiguus Thélohan, 1895	*Oreochromis niloticus* (Linnaeus, 1758)	Ho Chi Minh	FW	Skin	Oval-shaped, 0.5 × 0.2 mm	Pear-shaped; 10–11.4 (length) × 6.4–6.9 (width) × 4.5–5.5 (thickness); Fig. 18		Two PCs, pyriform-shaped, equal; 5.5–6.0 (length) × 1.8–2.3 (width)		K 2
Myxobolus hakyi (Ha, 1971) Landsberg & Lom, 1991	*Hypophthalmichthys harmandi* Sauvage, 1884	Bac Giang, Bac Ninh	FW	Kidney		Oval-shaped; 14.4–16.2 (length) × 11.7–12.6 (width) × 9.0 (thickness); Fig. 19		Two PCs, pyriform-shaped, unequal; The bigger: 6.8–7.2 (length) × 3.6 (width). The smaller: 4.5 (length) × 1.8 (width)	The bigger, 7 turns	K
Myxobolus hoabinhensis Chinh, Tham, Yurakno, Doanh, Whipps & Shirakashi, 2022	*Carassius auratus* (Linnaeus, 1758)	Hoa Binh	FW	Trunk muscle	Not observed	Ovoid-shaped; 11.4–12.6 (length) × 7.9–9.0 (width) × 5.8–6.3 (thickness); Fig. 20	MH790285	Two PCs, pyriform-shaped, unequal; The bigger 7.1–8.4 (length) × 3.3–3.8 (width). The smaller 5.5–6.7 (length) × 2.6–3.4(width)	The bigger4–5 turns; the smaller 3–4 turns	C a
Myxobolus humilis Ky, 1971	*Hypophthalmichthys harmandi* Sauvage, 1884	Bac Giang, Bac Ninh	FW	Spleen		Oval-shaped; 8.1–9 (length) × 6.3–7.2 (width); Fig. 21		Two PCs, pyriform-shaped, equal; 3.6–3.8 (length) × 1.8–2.7 (width)		K
Myxobolus koi Kudo, 1919	*Cyprinus carpio* Linnaeus, 1758); *Labeo rohita* (Hamilton, 1822); *Cirrhinus mrigala* (Hamilton, 1822)	Hai Phong, Quang Ninh, Ha Noi, Bac Ninh, Bac Giang	FW	Gill	Circle-shaped, 0.07–0.35 mm in diameter	Pear-shaped; 14.4–15.5 (length) × 7–8 (width) × 5–6.5 (thickness); Fig. 22		Two PCs, pyriform-shaped, equal; 7.2–8.2 (length) × 2.7 (width)		K 2
Myxobolus lanfuongi Ky 1971	*Spinibarbus denticulatus* (Oshima, 1926)	Bac Can	FW	Intestine	Spherical-shaped	Spherical-shaped; 10.8–11.7 mm in diameter; Fig. 23		Two PCs, pyriform-shaped, equal; 4.4–5.5 (length) × 2.7–3.6 (width)	7 turns	K
Myxobolus macrocapsularis Reuss, 1906	*Barbodes gonionotus* (Bleeker, 1849)	Mekong river delta	FW	Gill	Spherical-shaped, 0.45–0.55 mm in diameter	Pear-shaped; 10.9–11.6 (length) × 7.2 (width) × 6.2 (thickness); Fig. 24		Two PCs, pyriform-shaped, equal; 6.2 (length) × 2.3 (width)		K 2

Parasite	Host	Locality	Habitat	Infection site	Vegetative stage	Spore	GenBank	Polar capsule	Polar filament	F
Myxobolus minutus Ky, 1971	*Labeo rohita* (Hamilton, 1822); *Cirrhinus mrigala* (Hamilton, 1822)	Ho Chi Minh	FW	Gill	Circle-shaped, 0.26–1 mm in diameter	Pear-shaped; 10–13.5 (length) × 9–11.7 (width) × 8.6 (thickness); Fig. 25		Two PCs, pyriform-shaped, equal; 4.5–5.4 (length) × 2.7–3.6 (width)	57.6–68.4 μm in length	K
Myxobolus miyairii Kudo, 1919	*Pangasianodon hypophthalmus* (Sauvage, 1878)	Dong Thap	FW	Skin	Oval-shaped	Pear-shaped; 15.5–17 (length) × 7.8 (width) × 4.7–6.2 (thickness); Fig. 26		Two PCs, pyriform-shaped, equal; 6.2 (length) × 1.6–2.8 (width)	4 turns, 46 μm in length	K 2
Myxobolus oblongus Gurley, 1893	*Channa micropeltes* (Cuvier, 1831)	Mekong river delta	FW	Skin	Oval-shaped	Pear-shaped; 10.2–11.8 (length) ×7.7–8.7 (width) × 6.4 (thickness); Fig. 27		Two PCs, pyriform-shaped, equal; 3.6–4.1 (length) × 2.0–2.5 (width)	4 turns	K 2
Myxobolus pavlovskii (Achmerov, 1954)	*Hypophthalmichthys harmandi* Sauvage, 1884	Bac Ninh, Bac Giang, Ha Noi	FW	Body, Gill		10–11 (length) × 9–10 (width) × 7.2 (thickness); Fig. 28		Two PCs, pyriform-shaped, unequal; The larger: 6.3–7.2 (length) × 2.7–3.6 (width). The smaller: 3.6–5.2 (length) × 1.5–2 (width)		K 2
Myxobolus poljianskii Schulman, 1962	*Ompok bimaculatus* (Bloch, 1794)	Mekong river delta	FW	Gill		Oval-shaped; 14–17 (length) × 7.5 (width) × 4.7 (thickness); Fig. 29		Two PCs, pyriform-shaped, equal; 8.5 (length) × 3.1 (width)	7 turns	K 2
Myxobolus semeniformis Ky 1971	*Cirrhinus molitorella* (Valenciennes, 1844); *Cirrhinus mrigala* (Hamilton, 1822); *Labeo rohita* (Hamilton, 1822)	Ha Noi, Bac Ninh, Bac Giang, Tien Giang, Ho Chi Minh	FW	Gill, Skin	Circle-shaped, 4 mm in diameter	Pear-shaped; 13.2–14.4 (length) × 4.8–6 (width) × 3.6–4.2 (thickness); Fig. 30		Two PCs, pyriform-shaped, equal; 5.4–6.0 (length) × 1.4–1.8 (width)		K
Myxobolus spinacurvatura Maeno, Sorimachi, Ogawa & Egusa, 1990	*Mugil cephalus* Linnaeus, 1758	Khanh Hoa	M	Gall bladder, intestine	Circle-shaped, 0.2–3 in diameter	Oval/circle-shaped; 9.7–12.2 (length) × 8.1–9.8 (width) × 6.5 (thickness); Fig. 31		Two PCs, pyriform-shaped, equal; 4.1–5.3 (length) × 2.2–3.3 (width)	8.9–39.1 μm in length	Y & 2
Myxobolus toyamai Kudo, 1915	*Cyprinus carpio* Linnaeus, 1758	Bac Can, Bac Ninh, Bac Giang, Ha Noi, Ha Nam, Nam Dinh, Ninh Binh, Hung Yen, Quang Ninh	FW	Gill	Circle-shaped, 0.29–.55 in diameter	Oval-shaped; 15–18 (length) × 5.4 (width) × 4.5 (thickness); Fig. 32		Two PCs, pyriform-shaped, unequal; The larger: 9–10.3 (length) × 3.6 (width). The smaller: 3.6–4.5 (length) × 1 (width)		K 2

Parasite	Host	Locality	Habitat	Infection site	Vegetative stage	Spore	GenBank	Polar capsule	Polar filament	F
Myxobolus uyeni Ky, 1971	*Cirrhinus molitorella* (Valenciennes, 1844)	Lao Cai	FW	Intestine	Circle-shaped	Oval-shaped; 9.9–10.8 (length) × 8.8.5 (width); Fig. 33		Two PCs, pyriform-shaped, equal; 5.4 (length) × 2.7 (width)		K
Genus *Henneguya* Thélohan, 1892										
Henneguya hemibagri Tchang & Ma, 1993	*Hemibagrus nemurus* (Valenciennes, 1844)	Mekong river delta	FW	Gill, body	Oval or skeptical-shaped	Oval-shaped; Body 12.4 (length) × 4.7–6.2 (width); Fig. 34		Two PCs, pyriform-shaped, equal; 3.1 (length) × 2.3 (width)	3 turns	K 2
Henneguya lata Chinh, Ngo, Van Tuc, Itoh, Yoshinaga, Shirakashi & Doanh, 2021	*Acanthopagrus latus* (Houttuyn, 1782)	Quang Ninh	M	Gill	Rounded or ovoid-shaped, 0.15–0.2 mm in diameter	Elongate-shaped, smooth valves; Body 9.9 (8.9–12.5) (length) × 6.7 (6.1–7.6) (width) × 5.1 (4.8–5.4) (thickness). Two CAs, equal, 10.0 (8.3–11.6) (length). TL 19.3 (16.5–21.5); Fig. 35	MT644624; MT644625	Two PCs, ovoid-shaped, equal; 3.2 (2.8–3.9) (length) × 1.9 (1.5–2.3) (width)	4–5 turns	C a
Henneguya ophiocephali Chakrawarty, 1938	*Channa micropeltes* (Cuvier, 1831)	Mekong river delta	FW	Gill, Gall bladder	Oval-shaped	Oval-shaped; Body 12.7–13.8 (length) × 6.1–6.6 (width) × 3.1 (thickness). Two CAs equal, 25–45 (length). Figure 36		Two PCs, pyriform-shaped, equal; 6.1–6.6 (length) × 2.8 (width)	4 turns	K 2
Henneguya schizura (Gurley, 1893)	*Trichoporus trichopterus* (Pallas, 1770)	Mekong river delta	FW	Gill	Oval-shaped	Oval-shaped; Body 14.4–16 (length) × 8 (width). Two CAs equal, 40 (length). Figure 37		Two PCs, pyriform-shaped, equal; 4.8–5.6 (length) × 1.6 (width)	4 turns, 24 μm in length	K 2
Henneguya schulmani Ky, 1971	*Anabas testudineus* (Bloch, 1792)	Mekong river delta	FW	Gill	Oval-shaped, 0.25–0.3 mm	Oval-shaped; 16.8–20.4 (length) × 4.8–6 (width) × 3.6–4.2 (thickness). Figure 38		Two PCs, pear-shaped, equal; 8–10.2 (length) × 1.44–2.16 (width)		K
Henneguya shaharini Shariff, 1982	*Oxyeleotris marmorata* (Bleeker, 1852); *Oxyeleotris siamensis* (Güther, 1861)	Mekong river delta	FW	Gill	Oval or spherical-shaped	Oval-shaped; Body 12.4–14 (length) × 4.7–6.2 (width) × 3.9 (thickness). Two CAs equal, 14–15.5 (length); Fig. 39		Two PCs, pear-shaped, equal; 6.2–7.5 (length) × 1.6–2.3 (width)	6 turns, 17 μm in length	K 2
Genus *Thelohanellus* Kudo, 1933										
Thelohanellus acuminatus Ky, 1971	*Cyprinus carpio* (Linnaeus, 1758)	Hai Phong, Bac Ninh, Bac Giang, Ha Noi	FW	Gill	Spherical-shaped	Pear-shaped; 19.8–21.6 (length) ×7.2–8.1 (width); Fig. 40		One PC, pear-shaped; 4.5–5.4 in diameter		K

Parasite	Host	Locality	Habitat	Infection site	Vegetative stage	Spore	GenBank	Polar capsule	Polar filament	F
Thelohanellus callisporis Ky, 1971	*Cyprinus carpio* (Linnaeus, 1758)	Ha Noi, Bac Ninh, Bac Giang, Hai Duong, Hung Yen	FW	Skin, gill		Oval-shaped; 23.4–25.2 (length) × 12.6–16.2 (width) × 12.2 (thickness); Fig. 41		One PC, oval-shaped; 10.8 (length) ×7.2–8.1 (width)		K
Thelohanellus catlae Chakravarty & Basu, 1948	*Cyprinus carpio* (Linnaeus, 1758); *Barbodes gonionotus* (Bleeker, 1849)	Ha Noi, Bac Ninh, Bac Giang, Cuu long detal	FW	Gill, skin	Spherical-shaped, 1,5 mm in diameter	Pear-shaped; 19.8 (length) × 9.9 (width) × 8.25 (thickness); Fig. 42		One PC, spherical-shaped; 9.9 in diameter		K 2
Thelohanellus dogieli Achmerov, 1955	*Cyprinus carpio* (Linnaeus, 1758)	Ha Noi, Bac Giang, Bac Ninh	FW	Gill, skin, intestine	Spherical-shaped, 0.3–3.0 mm in diameter	Egg-shaped; 20.35–23.1 (length) × 9.9 (width) × 9.9 (thickness); Fig. 43		One PC, spherical-shaped; 9.9 in diameter		K 2
Thelohanellus kitauei Egusa & Nakajima, 1981	*Cyprinus carpio* (Linnaeus, 1758)	Hai Duong	FW	Intestine	Spherical-shaped. 1.4–1.1 cm in diameter	Pear-shaped; 24.9 (length) × 9.6 (width); Fig. 44		One PC, oval-shaped; 16.9 (length) × 7.3 (width)	187.6 µm in length	T a
Family Trilosporidae Shulman, 1959										
Genus *Unicapsula* Davis, 1924										
Unicapsula andersenae Miller & Adlard, 2013	*Paramonacanthus japonicus* (Tilesius, 1809); *Boesemania microlepis* (Bleeker, 1858)▲	Quang Binh; Khanh Hoa▲	M	Skeletal muscles	Elliptical-shaped, 0.3 mm (width) × 0.8 mm (length).	Subspherical-shaped; 5.1 (4.5–5.4) (length) × 4.6 (3.6–5.3) (width); Fig. 45	OQ255613▲	Three PCs, spherical-shaped, unequal; one larger with 1.8 (1.4–2.3) (length) × 1.7 (1.3–2.1) (wide)		C a
Unicapsula pyramidata (Naidenova & Zaika, 1970)	*Nemipterus japonicus* (Bloch, 1791)	Quang Ninh	M	Skeletal muscles	Elliptical-shaped, 0.07 mm (width) × 0.14 mm (length).	Bilaterally symmetrical triangular; 5.9 (5.5–6.4) (length) × 7.4 (5.6–9.6) (width). Two CFAs, equal, 7.2–7.4 (length); GenBank: AB971675, AB971676; Fig. 46	AB971675; AB971676	Three PCs, spherical-shaped, unequal; The bigger, 2.2 (2.0–2.4) (diameter), Two smaller equal, 0.4–0.5 (diameter)		T e 2
Family Kudoidae Meglitsch, 1960										
Genus *Kudoa* Meglitsch, 1947										
Kudoa monodactyli Gunter, Cribb, Whipps & Adlard, 2006	*Monodactylus argenteus* (Linnaeus, 1758)	Quang Bình, Khanh Hoa	M	Skeletal muscles	Elliptical-shaped, 0.2–0.4 mm (width) × 0.5–0.7 mm (length).	Stellate-shaped in apical view; 8.7 (8.2–9.3) (length) × 9.0 (8.4–9.6) µm in width and 6.3 (6.2–6.4) (thickness); Fig. 47		Five PCs, elliptical-shaped, equal; 3.3 (3.1–3.5) (length) × 2.3 (2.2–2.4) (width)		Y e 2

Parasite	Host	Locality	Habitat	Infection site	Vegetative stage	Spore	GenBank	Polar capsule	Polar filament	F
Kudoa scomberomori Adlard, Bryant, Whipps & Kent, 2005	*Scomberomorus guttatus* (Bloch & Schneider, 1801)	Quang Binh	M	Skeletal muscles	Elliptical-shaped; 0.1—0.3 mm (width) × 0.4—0.7 mm (length).	Flower petal-shaped in apical view; 6.7 (6.5—6.76) (length) × 7.4 (7.3—7.6) (width) × 6.6 (6.4—6.7) (thickness); Fig. 48		Six PCs, elliptical-shaped, equal; 3.4 (3.3–3.5) (length) × 1.3 (1.1—1.5) (width)		C a
Kudoa igori Violetta, Elena, Chinh, Ha & Whipps, 2022	*Osteomugil cunnesius* (Valenciennes, 1836)	Khanh Hoa	M	Gall bladder	Not observed	Orbicular to quadrate-shaped; 4.56 ± 0.22 (4.18—4.56) (length) × 4.42 ± 0.39 (3.55—5.13) (thickness) × 5.74 ± 0.46 (4.66—6.50) (width); GenBank: OL339420; Fig. 49	OL339420	Four PCs, pyriform-shaped, slightly unequal; The biggest: 1.4 ± 0.1 (1.1—1.7) (length) × 1.0 ± 0.1 (0.8—1.4) (width); the middle: 1.3 ± 0.12 (1.0—1.5) (length) × 0.9 ± 0.1 (0.8—1.1); the smallest PC: 1.1 ± 0.1 (0.9—1.3) × 0.7 ± 0.1 (0.6—0.9) (width)		Y e 2
Kudoa borimiri Violetta, Elena, Chinh, Ha & Whipps, 2022	*Osteomugil cunnesius; Osteomugil perusii*	Khanh Hoa	M	Skeletal muscles	Not observed	Quadrate-shape; 3.5 ± 0.2 (3.3—3.9) (length) × 3.7 ± 0.4 (2.8—4.2) (thickness) × 5.0 ± 0.4 (4.1—6.0) (width). GenBank: OL339422; Fig. 50	OL339422	Four PCs, pyriform-shaped, equal; 0.2 ± 0.2 (1.0—1.6) (length) × 0.9 ± 0.1 (0.7–1.0) (width)		Y e 2
Kudoa thyrsites (Gilchrist, 1924)	*Decapterus russeli* (Rüppell, 1830)	Khanh Hoa	M	Skeletal muscles	Not observed	Stellate shaped in apical view, pyramidal with a rounded pile in lateral view; 7.4 ± 0.4 (6.8—8.0) (length) × 13.8 ± 1.2 (11.5—16.4) (width max), 11.8 ± 0.9 (10.3—13.4) (width min) × 9.3 ± 1.0 (7.5—11.4) (thickness); GenBank: OL339424; Fig. 51	OL339424	Four PCs, pyriform-shaped, unequal; a biggest PC: 4.7 ± 0.8 (3.2—6.7) (length) × 3.6 ± 0.4 (2.0—4.2) (width); two middle: 3.5 ± 0.6 (2.8—4.9) (length) × 2.0 ± 0.1 (1.7—2.3) (length); a smallest: 2.6 ± 0.8 (1.6–4.2) (length) × 1.8 ± 0.2 (1.5—2.1) (width)		Y e 2

Parasite	Host	Locality	Habitat	Infection site	Vegetative stage	Spore	GenBank	Polar capsule	Polar filament	F
Kudoa whippsi Burger & Adlard, 2010	*Osteomugil cunnesius* (Valenciennes, 1836); *Osteomugil perusii* (Valenciennes, 1836)	Khanh Hoa	M	Skeletal muscles	Not observed	Star-shaped in above view, pyramidal shaped in side view; 5.0 ± 0.3 (4.6–5.6) (length) × 6.4 ± 0.8 (4.5–7.5) (thickness) × 8.8 ± 0.7 (7.5–10.2) width; GenBank: OL339425; Fig. 52	OL339425	Four PCs, pyriform-shaped, unequal; a biggest: 3.5 ± 0.4 (2.9–4.2) (length) × 2.3 ± 0.3 (1.8–2.8) (width); two middle: 2.3 ± 0.3 (1.8–2.8) (length) × 1.3 ± 0.1 (1.1–1.5) (width); a smallest PC: 1.6 ± 0.3 (11.7–2.1) (length) × 1.2 ± 0.1 (1.1–1.4) (width).		Y e 2

Results

A total of 51 myxosporean species belonging to 9 genera were listed as follow: *Myxobolus* (26 species), *Kudoa* (6 species), *Henneguya* (6 species), *Thelohanellus* (5 species), *Unicapsula* (2 species), *Ceratomyxa* (2 species), *Zschokkella* (2 species), *Auerbachia* (1 species), and *Meglitschia* (1 species). These comprised of 38 freshwater species and 13 marine species. The DNA sequence data of *Unicapsula andersenae* was 1361 base pairs in length and deposited in GenBank under the accession number OQ255613. The myxosporean species were mainly recorded in provinces in Red river and Mekong river deltas (Fig. 1). The features of each species are presented in Table 1 and illustrated in Figs. 2–52.

Discussion

To the best of our knowledge, most myxosporean species recorded in Vietnam have been identified solely by morphological analysis and their hosts, except for those reported within the last decade. A challenge in interpreting some spore measurement data from previous reports is the lack of detailed information as to whether fresh or fixed specimens were used for morphological examination (Ky, 1971). The impact of fixation on spore morphology has been well documented, as some fixatives (e.g. formalin, ethanol) cause reductions in spore size and distortions of spore shape (Kudo, 1921; Polyanskii, 1955; Parker & Warner, 1970). Therefore, caution should be exercised when comparing the size data between fresh and fixed materials, and even greater caution is needed when data lacks the information on use (or not) of fixatives. In addition, inconsistent use of morphometric terminology for species description create further confusion, as we indicated in a recent study (Chinh et al., 2022a). For instance, Vo et al. (2012) and Ky & Te (2007) used the terms “length” and “width” instead of the universal terms “thickness” and “length”, respectively, for the description of ceratomyxids (Ky & Te, 2007; Vo et al., 2012).

In Vietnam, myxospores in marine fish were first recorded in the Grouper (*Epinephelus* spp.) and Sea bass (*Lates calcarifer*) in Nha Trang (Khanh Hoa province) by Vo et al. (2012) who also recorded nine unidentified myxosporean species. However, the data in this book are insufficient and lack reliability for comparative purposes (discussed in Chinh et al., 2022a). For instance, *Meglitschia insolita* was listed in this book without information on spore measurements (Vo et al., 2012). It is likely that this species was identified based solely on the host fish species. Additional collections are necessary to evaluate and characterize these reports.

Recently, Truong et al. (2022) provided a comprehensive parasite list from Vietnamese marine fish. However, only 7 myxosporean species (including 3 unidentified species) were listed in their review (Truong et al., 2022). One identified species listed in their review, *Henneguya cerebralis*, needs further consideration. *Henneguya cerebralis* was recorded on the cranial skin and head cartilage of three grayling species (*Thymallus nigrescens*, *Thymallus brevirostris*, and *Thymallus baicalensis*) from the basin of Lake Baikal and the West Mongolian Province (Pronin, 1971; Gundrizer, 1976; Batueva et al., 2013). However, in Vietnam, this species was recorded in the gill of Sea bass *L. calcarifer* in Nha Trang (Khanh Hoa province). Given the lack of morphological data on the report of *H. cerebralis* in Vietnam, and the differences in geography, host, and host tissue, we suspect that this *Henneguya* species reported from Sea bass in Vietnam is not *H. cerebralis*, and that this needs to be revisited in other future studies. Thus, *H. cerebralis* is not listed in this review.

Reviewing the past literature has led us to discover a nomenclature issue regarding Vietnamese myxospores. In 1971, *Myxobolus asymmetricus* was described from *Hypophthalmichthys harmandi* in Vietnam by Ha (1971). Later, *Myxobolus* and *Myxosoma* were synonymized by Landsberg & Lom (1991), and *Myxobolus asymmetricus* became junior synonym for *Myxosoma asymmetrica*, a species described by Parisi (1912) from *Crenilabrus pavo* (originally described as *Lentospora asymmetrica*) in Italy. To resolve this, Landsberg & Lom (1991) proposed a new name for this Vietnamese species, *Myxobolus hakyi*. Unfortunately, the taxonomic confusion with this name was compounded further when Baska et al. (2009) used the preoccupied name *M. hakyi* to describe a myxozoan species from the skin of *Pangasianodon hypophthalmus* in Thailand, which is a junior homonym for the Vietnamese *M. hakyi*. To resolve this, we propose the replacement name *Myxobolus eszterbaueri* nomen novum for the species described by Baska et al. (2009). The name honours Dr. Edit Eszterbauer, a highly respected myxozoan species researcher, and coauthor of the Baska et al. paper.

In conclusion, based on all the documents assessed, we listed 51 nominal myxosporean species parasitizing freshwater and marine fishes collected from different localities in Vietnam. This synopsis provides useful information for future references and species identification, including Vietnamese hosts, organ infected, measurement, and line draw illustrations of myxospores. The majority of Vietnamese myxosporean samples have mainly been collected from freshwater fishes in the two biggest deltas of Vietnam (Red river and Mekong river deltas). Our synopsis highlights areas where sampling has been poor or non-existent, allowing for more strategic sampling. In the future, studying myxosporean parasites from coastal water regions and other areas on the mainland of Vietnam will most likely led to the discovery of more species. Research on myxosporeans are still insufficient in Vietnam, but such study will provide important information about parasite biodiversity and risk management for the aquaculture of Vietnam.

Declarations

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Author contributions: N.N.C. wrote the first draft of the manuscript, prepared figures 2-52, and created manuscript table 1. N.T.H.H. prepared figure 1 and generated DNA sequence data for *Unicapsula andersenae*. P.N.D., J.C.E., C.M.W., and S.S. revised and improved the manuscript and table 1. N.N.C. oversaw all subsequent revisions of the manuscript and wrote the final version for journal review. All authors reviewed the manuscript and provided edits on the final version.

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Figures

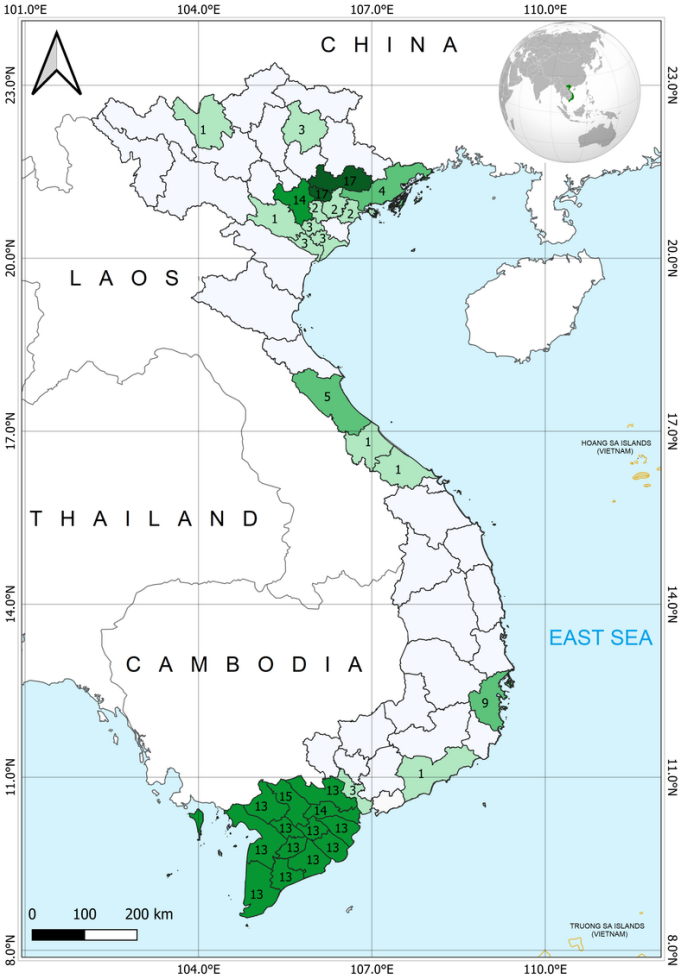

Figure 1

Number of recorded myxosporean species per province in Vietnam

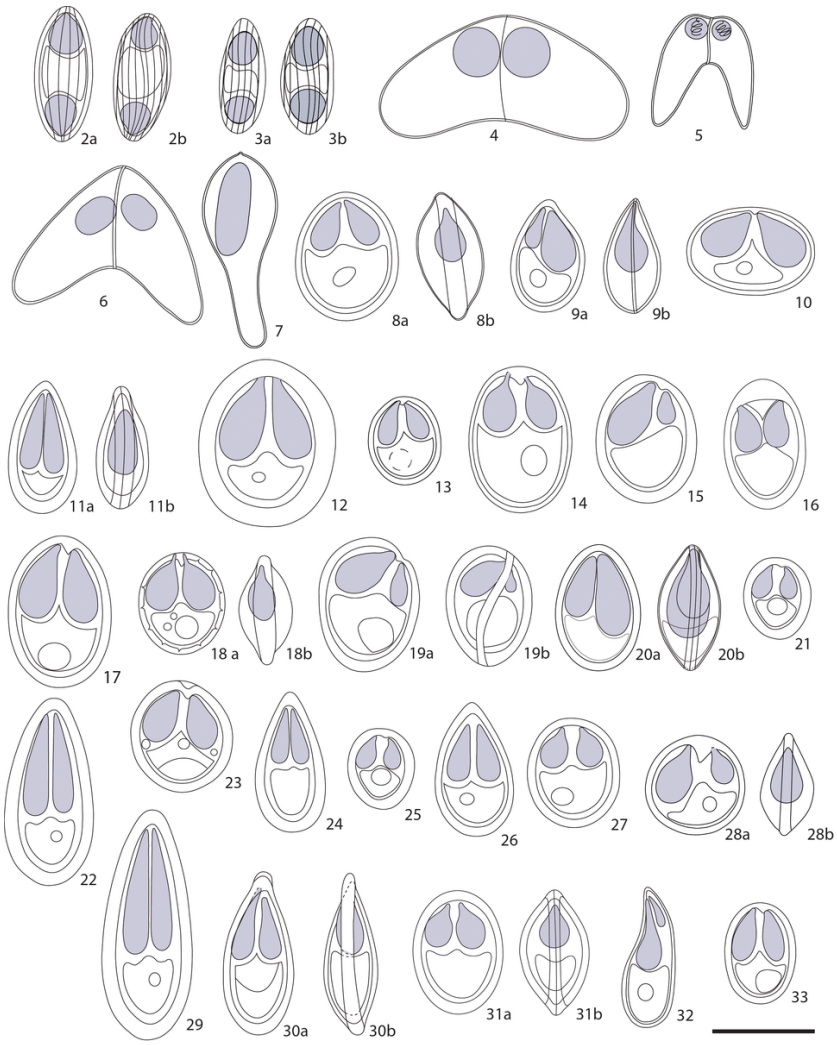

Figure 2

The representative drawing of myxosporean species in *Zschokkella, Ceratomyxa, Meglitschia* and *Myxobolus* genus.

2, *Zschokkella donetzae*; 3, *Zschokkella orientalis*; 4, *Ceratomyxa binhthuanensis*; 5, *Ceratomyxa tienensis*; 6, *Meglitschia insolita*; 7, *Auerbachia chakravartyi*; 8, *Myxobolus achmerovi*; 9, *Myxobolus anisocapsularis*; 10, *Myxobolus artus*; 11, *Myxobolus cheisini*; 12, *Myxobolus clarii*; 13, *Myxobolus cyprini*; 14, *Myxobolus cyprinicola*; 15, *Myxobolus discapsularis*; 16, *Myxobolus divergens*; 17, *Myxobolus ellipticus*; 18, *Myxobolus exiguus*; 19, *Myxobolus hakyi*; 20, *Myxobolus hoabinhensis*; 21, *Myxobolus humilis*; 22, *Myxobolus koi*; 23, *Myxobolus lanfuongi*; 24, *Myxobolus macrocapsularis*; 25, *Myxobolus minutus*; 26, *Myxobolus miyairii*; 27, *Myxobolus oblongus*; 28, *Myxobolus pavlovskii*; 29, *Myxobolus poljianskii*; 30, *Myxobolus semeniformis*; 31, *Myxobolus spinacurvatura*; 32, *Myxobolus toyamai*; 33, *Myxobolus uyeni*. Scale bar: 10 μm.

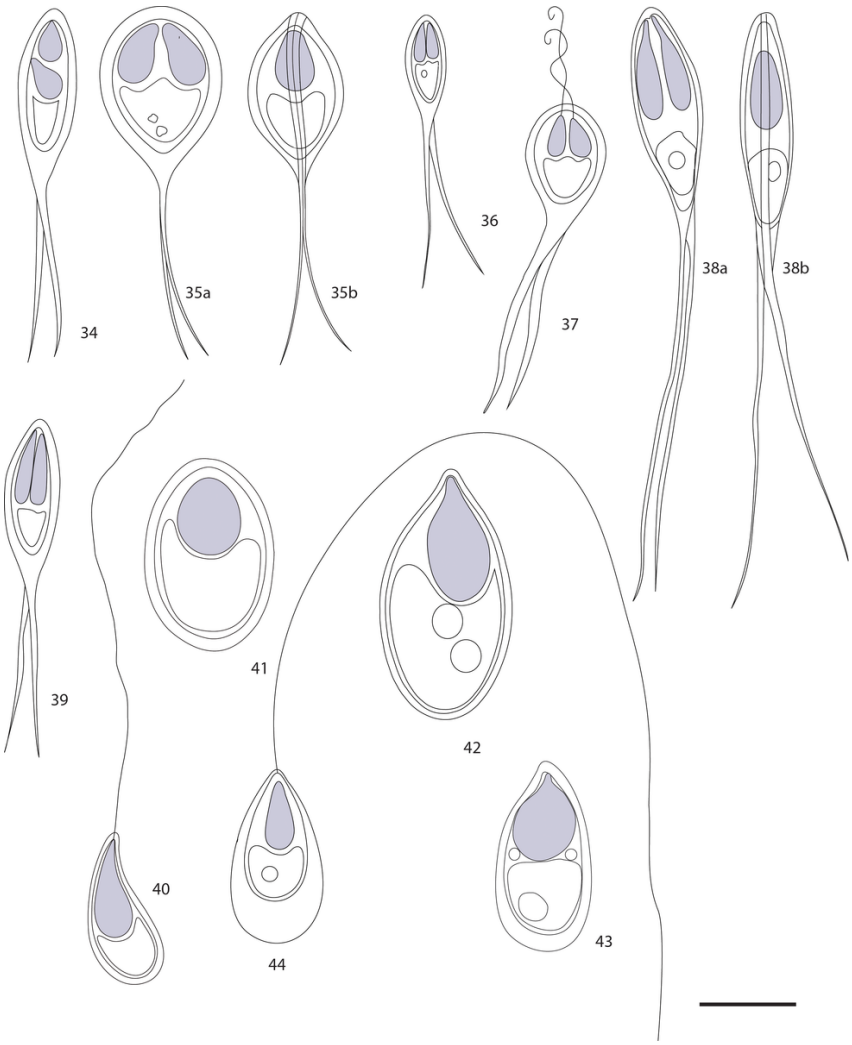

Figure 3

The representative drawing of myxosporean species in *Henneguya* and *Thelohanellus* genus.

34, *Henneguya hemibagri*; 35, *Henneguya lata*; 36, *Henneguya ophiocephali*; 37, *Henneguya schizura*; 38, *Henneguya schulmani*; 39, *Henneguya shaharini*; 40, *Thelohanellus acuminatus*; 41, *Thelohanellus callisporis*; 42, *Thelohanellus catlae*; 43, *Thelohanellus dogieli*; 44, *Thelohanellus kitauei*. Scale bar: 10 μm.

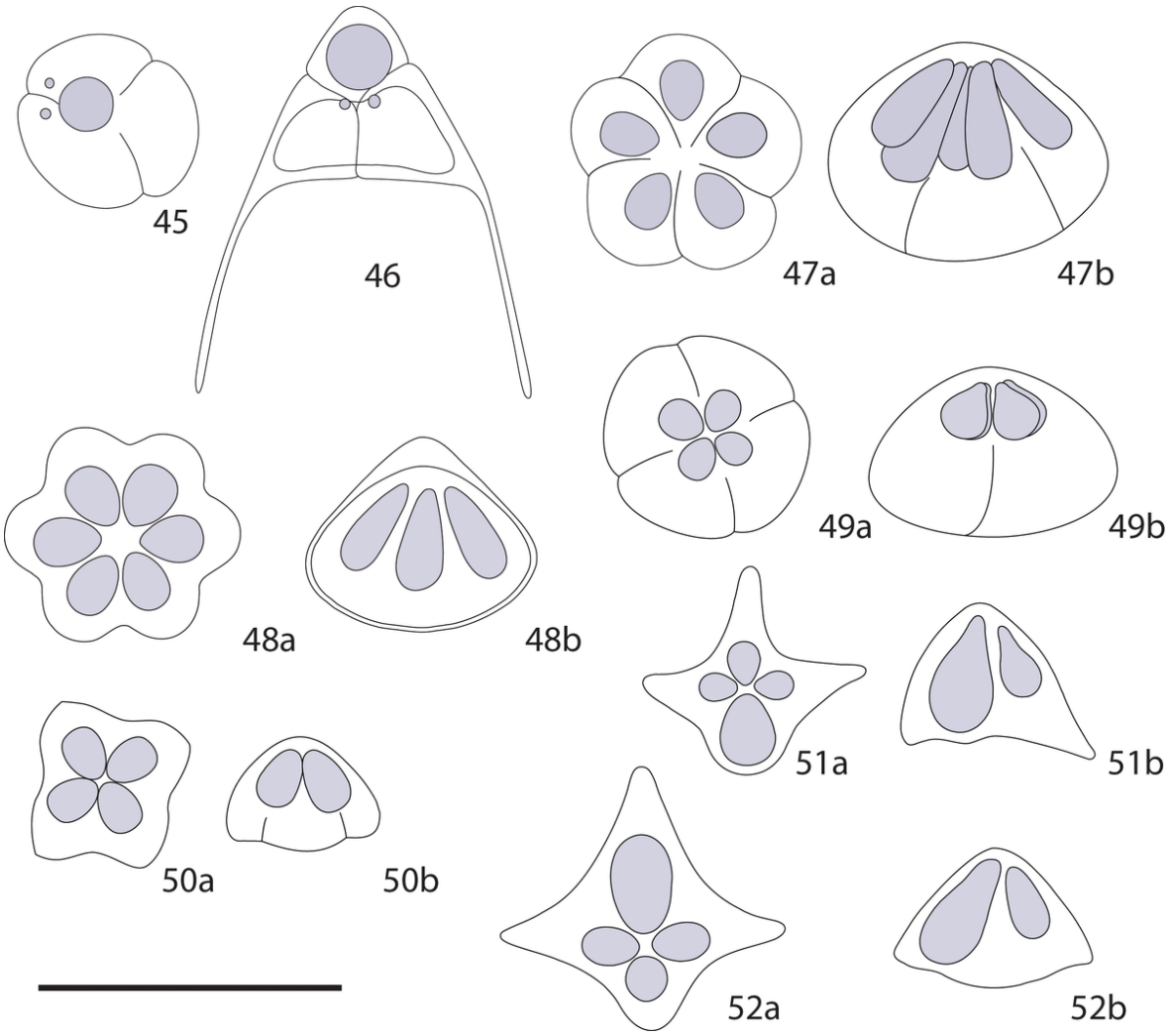

Figure 4

The representative drawing of myxosporean species in *Unicapsula* and *Kudoa* genus.

45, *Unicapsula andersenae*; 46, *Unicapsula pyramidata*; 47, *Kudoa monodactyli*; 48, *Kudoa scomberomori*; 49, *Kudoa igori*; 50, *Kudoa borimiri*; 51, *Kudoa thyrsites*; 52, *Kudoa whippsi*. Scale bar: 10 μm.