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ORIGINAL PAPER

Structural and molecular characterization of *Kudoa quraishii* n. sp. from the trunk muscle of the Indian mackerel *Rastrelliger kanagurta* (Perciforme, Scombridae) in Saudi Arabia coasts

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Abstract A new Myxozoa, *Kudoa quraishii* n. sp., is reported in the striated muscle of the Indian mackerel *Rastrelliger kanagurta* from the Red Sea and the Arabian Gulf in Saudi Arabia. Mean prevalence of infection is about 20 % and varies between localities. The parasite develops whitish and oval or rounded pseudocysts of 0.2–3 mm in the striated muscles of the body. Pseudocysts are filled with mature spores. Myxospores are quadrate in shape in apical view with rounded edges and ovoid in side view. Each spore is formed by four equal shell valves and four symmetrical polar capsules. Polar capsules are pyriform in apical view and drop-like in side view. Myxospore measurements in micrometers are 6.14 (5.9–6.34) in width, 5.48 (5.3–5.71) in thickness, and 4.27 (4.1–4.42) in length. Polar capsule measurements in apical view in micrometers are 2.08 (1.88–2.28) and 1.31 (1.10–1.52) length by width. Molecular analysis based on SSU rDNA gene shows closest association with *K. amamiensis* and *K. kenti* with respectively 98 and 97.2 % of similarities.

Introduction

Kudoa is actually the largest genus in the order of Multivalvulida with more than 80 species (Moran et al. 1999b; Kent et al. 2001; Lom and Dykova 2006). In fact, since the demise of the order of Pentacapsulidae Naidenova and Zaika 1970, Hexacapsulidae Shulman 1959, and Septemcapsulidae Hsieh and Chen 1984, all the species with more than four valves were affected to the *Kudoa* genus, which became the single genus in the family of Kudoidae (Whipps et al. 2004). This revision in the order of Multivalvulida has only been possible by the use of molecular tools in the characterization of Myxozoa parasites based mainly on the sequence analysis of the SSU rDNA gene (Hervio et al. 1997; Andree et al. 1999; Xiao and Desser 2000; Kent et al. 2001; Canning and Okamura 2004; Whipps et al. 2004). Therefore, the genus of *Kudoa* was defined as a group of Myxozoa parasites having four or more valves and polar capsules. Before the use of molecular tools, characterization was mainly based on spore morphology and measurements and second on the host species, its geography and the infected tissue. In this situation, some *Kudoa* parasites were affected to new species because of slight differences in morphology or measurements of spore or geography distribution. This was the case for example of *Kudoa thyrsites* reported firstly in *Scomber japonicus* as *Kudoa histolytica*, and *Kudoa nova* reported by some authors as *Kudoa quadratum* in carangid fish (Perard 1928; Moran et al. 1999b; Shukhgalter 2004; Whipps and Kent 2006; Levsen et al. 2008). Thereby, actually consistent characterization should take into account morphometric data of the spore, information about the infected host and its geography, site of infection, histological data, ultrastructural information, and molecular data, particularly of the SSU rDNA gene and eventually LSU rDNA gene. However, information about the host, the site of infection, and molecular data alongside morphometric characterization are of critical importance (Burger et al. 2007; Burger and Adlard 2010b; Heiniger et al. 2013). The main features currently collected on

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the genus of *Kudoa* show that they are essentially histozoiques species and often infect skeletal muscle forming unsightly cysts and causing postmortem myoliquefactive autolysis commonly referred to as soft flesh syndrome affecting the marketability of commercially important fisheries (Egusa and Nakajima 1980; Egusa 1986; Langdon 1991; Lom and Dyková 1994; Moran et al. 1999a; Moran et al. 1999b). However, some species have been encountered in other organs such as the heart, brain, gills, intestines, ovary, and kidney (Sandeep et al. 1986; Swearer and Robertson 1999; Grossel et al. 2003; Reimschuessel et al. 2003; Yurakhno et al. 2007; Al Quraishy et al. 2008; Abdel-Ghaffar et al. 2009, 2012; Heiniger and Adlard 2012; Mansour et al. 2013). These parasites may affect fish health by causing certain diseases such as meningoencephalomyelitis caused by *Kudoa neurophila* (Grossel et al. 2003), heart failure as reported in the infection by *Kudoa pagrusi* (Abdel-Ghaffar et al. 2009), and infertility of eggs as caused by the infections with *Kudoa ovivora* (Schärer and Vizoso 2003). Recently, the importance of *Kudoa* parasites in public health has been reported by the implication of *Kudoa septempunctata* in a food poisoning disease in Japan population consuming raw olive flounder (Matsukane et al. 2010; Kawai et al. 2012).

In the Red Sea and Arabian Gulf, few *Kudoa* species was reported as *Kudoa aegyptia*, *K. pagrusi*, and *Kudoa* sp. infecting the hearts of the species *Rhabdosargus haffara*, *Pagrus pagrus*, and *Plectropomus maculatus*, respectively (Koura 2000; Al Quraishy et al. 2008; Abdel-Ghaffar et al. 2009, 2012), and *Kudoa iwatai* infecting muscle tissue and other organs of the European sea bass *Dicentrarchus labrax* (Diamant et al. 2005). Host specificity is variable among the genus *Kudoa*. About two thirds of reported species were found in a single host species. The rest of species were encountered in at least two different hosts (Burger and Adlard 2011). Within this group, some species have both worldwide distribution and wide host range. The highest number of host was recorded for the cosmopolitan parasite *K. thyrsites* with 38 different host species belonging to 18 different fish families representing nine fish orders (Whipps and Kent 2006), followed by *K. nova* with 23 host species (Gorchanok and Yurakhno 2005; Machkevsky and Gorchanok 2005; Pascual et al. 2012), *K. iwatai* with 19 (Egusa and Shiomitsu 1983; Sugiyama et al. 1999; Diamant et al. 2005; Matsukane et al. 2011), and *Kudoa thalassomi* with 18 (Burger and Adlard 2011). The low host specificity of some kudoid species could facilitate the spread of parasites and its transmission to the basin of fish farming.

The Indian mackerel *Rastrelliger kanagurta* Cuvier 1817 is an epipelagic, neritic Perciforme, Scombridae species occurring in areas where surface water temperatures are at least 17 °C. It is widespread in the Indo-West Pacific from South Africa, Seychelles, and the Red Sea east through Indonesia and off the northern Australia to Melanesia, Micronesia, Samoa, China, and the Ryukyu Islands. It has entered the eastern Mediterranean Sea through the Suez Canal (F.A.O 2000). This species is of high commercial value, especially in Southeast Asia and India playing important roles in ecosystem and bioprocess. The maximum fork length reported is 38 cm and the common is 25 cm (Collette and Nauen 1983). The size at first maturity is approximately 17–20 cm (Sivadas et al. 2006). The spawning season varies slightly between locations and seems to extend from March through September in India (Abdussamad et al. 2006). Growth is very fast especially in the juvenile stages and could reach a length of 19 cm by the end of the first year, and longevity is estimated to be approximately 4 years (Devaraj et al. 1997; Abdussamad et al. 2006; Sivadas et al. 2006; Ganga 2010).

Very few studies dealing with parasites infecting the Indian mackerel were reported. Most of these studies have been devoted to the description of metazoan parasites (Murugesh 1995; Ravichandran et al. 2009; Madhavi and Triveni Lakshmi 2012). Only one study dealing with Myxosporea infecting the gall bladder of *R. kanagurta* allowing the description of a new species *Pseudalataspora misrae* (Bivalvulida) has been recently reported in the Bay of Bengal (Sarkar 2012).

In the present study, we report a description of a new *Kudoa* species parasitizing the striated muscles of the Indian mackerel, *R. kanagurta*, from three different sites in the Saudi Arabia coasts.

Material and methods

Sample collection

Between May and September 2013, 128 specimens of the Indian mackerel *R. kanagurta* Cuvier, 1816, having 11.3–26.5 cm in length, were purchased from the commercial fish cat working in Jeddah (21° 32′ 36″ N 39°10′ 22″ E) and Jazan (16° 53′ 21″ N 42° 33′ 40″ E) in the Red Sea coasts and from Dammam (26° 17′ N 50° 12′ E) in the Arabian Gulf of Saudi Arabia. The examined fish were in a fresh state and have no any external symptoms. After external examination, all internal organs (liver, intestine, heart, gall bladder, kidney, etc.) and gills were extracted in petri dishes, examined under stereoscope, and fresh smears were observed under light microscope. Muscles were macerated, visualized under stereoscope, and all cysts were extracted, squashed between slide and coverslip and observed under light microscope. Identified Myxosporea cysts were collected using forceps, crushed in an Eppendorf tube containing phosphate buffer saline (PBS) 1×, and their content was verified under light microscope in different magnifications.

Histological and morphometric study

When cysts were detected, slices of 0.5 cm^2 of infected tissue were fixed in neutral buffered formalin, embedded in paraffin, and serial sections of 5 μm of thickness were prepared using standard histological techniques. Slides were stained with hematoxylin and eosin (H&E) and covered with coverslip. Digital light micrographs of the sections were taken at ×10, ×40 and ×100·magnifications.

Fresh wet mount preparations of myxospores were examined under a microscope equipped with digital camera (Olympus BX 51). Digital light micrographs were taken for a large number of spores from different preparations. Measurements with digital micrometer were realized using at least 30 spores according to the recommendations of Lom and Arthur (1989).

In addition, air-dried spores fixed with methanol and stained with May-Grunwald-Giemsa were examined in a light microscope and photographed.

For scanning electron microscopy, free spores were fixed 4 h in 2.5 % glutaraldehyde, washed three times with 1 M sodium cacodylate buffer, and then dehydrated in a graded ethanol series. The sample was then coated with gold and examined with a JEOL JSM-6380 LA.

Molecular analysis of SSU rDNA

Genomic DNA was extracted as reported by Mansour et al. (2013). Briefly, a suspension of 10^8–10^9 purified spores in PBS 1× were treated with the FastDNA® Kit (MP Biomedicals, LLC) according to the manufacture of the supplier. The quality and quantity of eluted DNA were verified with electrophoresis in agarose gel using a standardized DNA ladder marker (1 μg/μl) (Solis, BioDyne).

The partial 18S SSU rDNA gene was amplified and sequenced using the same primers used by Mansour et al. (2013); MyxF1338 (GACTCAACACGGGAAAACTTA), MyxR1437 (TGGCCGTTCTTAGTTCGTGGAGTGAT), MyxR1944 (CTTTGTACACACCGCCCGTCGC) (Mansour et al 2013) and MyxF144 (ACCGTGGGAAATCTAGAGCTAA), MyxF818 (GTGTGCCTTGAGTAAATCAGAGT), MyxR862 (TTGAATGTTGATAGCATGGAAC). PCR reactions were conducted in 30 μl in volume, using about 50 ng of genomic DNA, 0.2 pmol of each primer, 1× Taq DNA buffer (MBI, Fermentas), 0.2 mmol of mixed dNTP, 1.5 mmol of $MgCl_2$, and 1 unit of Taq polymerase (MBI, Fermentas).

The PCR amplifications were carried out in a thermal cycler apparatus (Techne TC-Plus Satellites). The PCR program used was as follows: initial denaturation at 95 °C for 4 min, 35 cycles of 94 °C for 30 s, 50 °C for 30 s, and 72 °C for 60 s and a final extension of 72 °C for 5 min.

Five microliters of PCR products was migrated in an agarose gel (1 %) in a Tris-borate-EDTA buffer (0.045 M Tris-borate, 0.001 M EDTA pH 8.0), stained with ethidium bromide, and visualized and photographed on an UV transilluminator using a gel documentation system (BioRad Gel Doc™ XR+).

PCR products were cleaned up with ExoSAP-IT® (Affymetrix, Inc.) and then sequenced using the ABI BigDye (3.1) Terminator v3.1 Cycle Sequencing Ready Reaction, using the ABI PRISM 3130 Genetic Analyzer (Applied Biosystems, California). Obtained sequences were assembled with CAP3 program (http://pbil.univ-lyon1.fr/cap3.php) (Huang and Madan 1999). A consensus sequence of 1,464 nucleotides (nt) was deposited in GenBank (accession no. KF413764).

Related 41 *Kudoa* SSU rDNA sequences were extracted from GenBank according to their BLAST homology score (Altschul et al. 1997) and aligned with default parameters of CLUSTAL X software version 2 (Thompson et al. 1997) (Table 1). Obtained alignment was used to create a phylogenetic tree with MEGA software version 5 (Tamura et al. 2011) using the maximum likelihood and neighbor joining methods. Bootstrap analysis was based on 1,000 resampling. For the maximum likelihood method, the tree was obtained with the highest log likelihood (−8705.2322). Distance matrix for transitions and transversions was estimated using the Kimura two-parameter model. Sequence of *Ellipsomyxa gobii* was used as outgroup.

Results

For all examined fish, cysts of *Kudoa* infections were detected in the striated muscle throughout the body. The parasite occurs with a prevalence of ~20.31 % (26/128). This prevalence is of 29.4 % (20/68) in Jeddah, 6.25 % (2/32) in Jazan, and 14.28 % (4/28) in Dammam. Among these 26 parasitized specimens, 23 were of male sex, 1 unsexed, and 2 female. Pseudocysts were whitish and rounded or ovoid and sized 0.2–1 by 0.3–2.5 mm (Fig. 1a–c). Some pseudocysts were localized in the muscles of the buccal cavity when removing gills and also in extraocular muscles (Fig. 1b, c).

Myxospores of *Kudoa quraishii* n. sp.

In a fresh preparation, myxospores of *K. quraishii* were quadrate in shape in apical with rounded edge and four equal sized valves (Fig. 2a). Each valve contains one polar capsule. The polar capsules were pyriform and of equal sizes. The sutural lines are conspicuous between valves. In side view, myxospores were ovoid, with a protruded apex and drop-like polar capsules (Fig. 2a–d). In Giemsa-stained spores, lateral extrusions of polar tubes were well observed (Fig. 2c). SEM examination shows spores without any projections at the anterior end of the spores (Fig. 2d).

Table1 Accession number and coordinates in SSU rDNA database entry for Myxosporea species used for multiple alignment and phylogenetic tree construction. Percentage of similarity is based on the Kimura two-parameter model obtained after pairwise analysis between *K.quraishii* and selected *Kudoa* parasites

Myxosporea species	Accession numbers	18S rDNA coordinates	Percentage of identity with *K.quraishii*
K.quraishii	KF413764	1-1463	ID
K.amamiensis	AF034638	117-1575	98.01
K.kenti	FJ792714	7-1468	97.19
K.scomberi	AB693044	118-1601	92.38
K.crumena	AF378347	118-1601	92.24
K.trachuri	AB553299	118-1615	92.22
K.hypoepicardialis	AY302722	118-1579	92.39
K.leptacanthae	JQ974029	87-1546	92.03
K.shiomitsui	AY302724	118-1577	91.9
K.iwatai	AB553295	118-1526	90.52
K.neurophila	AY172511	122-1537	88.73
K.ovivora	AY152750	118-1536	89.51
K.dianae	AF414692	118-1553	89.33
K.alliaria	DQ182561	118-1549	89.11
K.carcharhini	GU324970	93-1522	90.71
K.monodactyli	DQ439814	100-1541	87.57
K.quadricornis	FJ792721	130-1561	89.33
K.hemiscylli	GU324957	8-1444	90.71
K.nova	EF644198	38-1484	88.82
K.yasunagai	AY302741	118-1551	88.65
K.scomberomori	AY302737	118-1550	88.69
K.lateolabracis	AY382606	118-1554	88.79
K.paniformis	AF034640	116-1548	88.88
K.trifolia	AM183300.2	125-1541	90.01
K.cookii	JX090294	84-1497	88.98
K.thunni	AB553300	117-1615	92.11
K.megacapsula	AB188529	118-1549	88.91
K.neothunni	AB693042	308-1741	88.49
K.paraquadricornis	FJ792718	130-1561	89.33
K.irnonata	FJ790311	138-1568	89.52
K.thyrsites	AY941819	118-1549	88.85
K.whippsi	FJ792725	7-1446	88.79
K.thalassomi	AY302738	118-1550	88.85
K.minithyrsites	AY152749	114-1545	88.56
K.septempunctata	AB553293	118-1554	89.42
K.ciliatae	DQ519390	136-1566	89.03
K.permulticapsula	AY078429	118-1549	88.49
K.azevedoi	HQ540316	1-1425	87.21
K.chaetodoni	JQ026218	83-1517	88.72
K.lethrini	DQ519388	136-1568	88.79
Ellipsomyxa gobii	GQ229236	128-1571	82.91

Ellipsomyxa gobii is used as outgroup

Dimensions of spore preserved in phosphate buffer saline based on 30 measurements for average±standard deviation (range) in micrometers are 6.14±0.38 (5.9–6.34) in width, 5.48±0.32 (5.3–5.7) in thickness, 4.27±0.38 (4.1–4.42) in length, 2.08±0.29 (1.88–2.28) in polar capsule length, and 1.31±0.22 (1.10–1.52) in polar capsule width (Table 2).

Histological examination shows pseudocysts surrounded with a thin layer of fibrous elements and filled with myxospores (Fig. 3a). Local lyses of myofibers around pseudocysts were observed without inflammatory reaction (Fig. 3b, c).

A blast research of the 1,464 nt obtained sequence of *K. quraishii* indicates that the highest similar Myoxosporea sequences are those of *Kudoa amamiensis* (97.98 to 98.26 %) and *Kudoa kenti* (97.2 %) (Table 1). The phylogenic trees inferred by maximum likelihood and neighbor joining are similar and confirm the closest association of *K. quraishii* with *K. amamiensis* and *K. kenti* with high bootstraps values (Fig. 4a). A subtree of different deposited sequences of *K. amamiensis* and *K. kenti* shows three different branches, one for the cluster of 12 *K. amamiensis* isolates, one for the two *K. kenti* isolates, and a third branch for *K. quraishii* (Fig. 4b). For all *K. amamiensis* sequences, the percentage of similarity with *K. quraishii* varies between 97.98 and 98.26 % (Table 3). These percentages were of 97.13 and 97.2 % with the two *K. kenti* isolates. The number of differences in nucleotides over the 1,464 bases was 21 nt to 25 nt with *K. amamiensis* isolates and of 38 nt or 39 nt with *K. kenti* isolates (Table 3).

Taxonomic summary

Phylum: Myxozoa Grassé 1970

Class: Myxosporea Bütschli 1881

Order: Multivalvulida Shulman 1959

Genus: *Kudoa* Meglitsch 1947

Host: *Rastrelliger kanagurta* Cuvier, 1816, Indian mackerel (Teleostei, Perciforme, Scombridae).

Localities: Red Sea and Arabian Gulf of Saudi Arabia coasts.

Site of infection: cysts in trunk muscles.

Prevalence: ~20 %

Materials deposited: One slide of serial histological sections of infected tissue (ZS119) and one slide of Giemsa-stained smear of spores (ZS120) were deposited in the Protists Collection of the Natural History Museums of Paris, France. Small subunit ribosomal DNA sequence was deposited in GenBank (accession number, KF413764).

Etymology: The specific name is dedicated to Dr. Salah Al-Quraishy, eminent fish parasitologist in the Department of Zoology of the College of Sciences, King Saud University of Riyadh, Saudi Arabia.

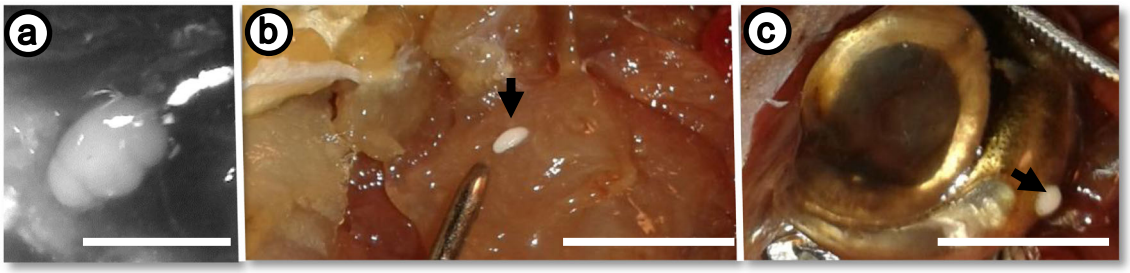

Fig. 1 Light photomicrographs of pseudocysts encountered in the muscles of *R. kanagurta*. **a** External morphology of extracted cyst. **b** Ovoid cysts in the muscle of the body. **c** Rounded cysts in the extraocular muscles (*arrowhead*). *Scale bars*: **a** 0.5 cm; **b**, **c** 1 cm

Discussion

The Myxozoa reported herein presents all the characteristics of the genus *Kudoa* Meglitsch, 1947. Structural and molecular data combined with geography and infected host demonstrate that the present parasite is a new *Kudoa* species, named *K. quraishii* n. sp. Considering the host *R. kanagurta* (Perciformes, Scombridae), no *Kudoa* parasites were reported elsewhere, and the only Myxosporea species was *P. misrae* (Bivalvulida) described in India (Sarkar 2012). To our knowledge, eight *Kudoa* species with four valves have been reported in the family of Scombridae. Among these species, two are widely distributed with low host specificity, infecting a large number of fish species belonging to different families. This is the case of *K. nova* Naidenova 1975 reported in 23 different species including two Scombridae: *Thynnus obesus* and *Euthunnus alleteratus*, and *K. thyrsites* Gilchrist 1924 recorded in at least 38 species of which *Scomber scombrus*, a sister species of *R. kanagurta* (Moran et al. 1999b; Burger and Adlard 2011). The remainder six *Kudoa* species are *Kudoa scomberi* (Li et al. 2013), *Kudoa caudata* (Kovaleva and Gaevskaya 1983), *Kudoa crumena* (Iversen and Van Meter 1967), *Kudoa thunni* (Matsukane et al. 2011), *Kudoa clupeidae* (Reimschuessel et al. 2003), and *Kudoa shiomitsui* (Egusa and Shiomitsu 1983). Except for *K. shiomitsui*, reported in the heart muscles of *Thunnus orientalis* and *Takifugu rubripes* (Egusa and Shiomitsu 1983; Zhang et al. 2010), the other five *Kudoa* species were identified as parasites of the trunk muscles of four Scombridae species: *S. japonicus*, *Scomberomorus maculatus*, *Thunnus alalunga*, and *Thunnus thynnus*, respectively. Comparison of morphometric data between *K. quraishii* and all the described species in Scombridae hosts shows that except for *K. nova*, which should have measurements of spore in the range of those of *K. quraishii*, all the other species were of higher dimensions (Table 2). The widely distributed species *K. thyrsites* recognized by stellate spores and unequal polar capsules previously reported in *S. scombrus* as *Kudoa histolyticum* are so far different to the present species (Perard 1928; Levsen et al. 2008). *K. caudata* has a thicker spore and characterized by stripes on the lower lateral surface of each valve. Comparison with other *Kudoa* species reveals similarities in size with *K. amamiensis* (Egusa and Nakajima 1980), *Kudoa azoni* (Aseeva 2004), *Kudoa sebastea* (Aseeva 2004), *K. kenti* (Burger and Adlard 2010a), *Kudoa trachuri* (Matsukane et al. 2011), *K. pagrusi* (Al Quraishy et al. 2008; Abdel-Ghaffar et al. 2009), *Kudoa* sp. (Abdel-Ghaffar et al. 2012), and *Kudoa leptacanthae* (Heiniger and Adlard 2012). Only *K. amamiensis* seems to be closely similar either in morphology aspects or measurements. For spore measurements, *K. quraishii* is slightly smaller than *K. amamiensis* isolated from different fish hosts in Australia (Burger et al. 2008) but nearly similar to those described in Japan by

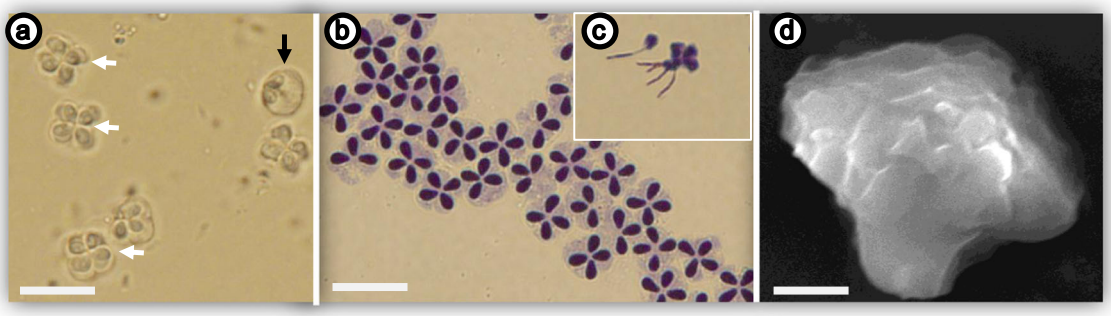

Fig. 2 Photomicrographs of spores of *Kudoa quraishii* from *R. kanagurta*. **a** Fresh smear showing spores in apical view (*white arrows*) and side view (*black arrows*). **b** MGG-stained spores. **c** Stained spore with polar filaments extruded. **d** SEM of mature spore in side view. *Scale bars*: **a**, **b** 10 μm; **d** 1 μm

Table 2 Morphometric comparison between *Kudoa quraishii* n. sp. and other similar *Kudoa* species (range in parentheses)

Kudoa species	Host/organ	Locality	Width	Thickness	Length	Polar capsule: length/width	Reference
Kudoa quraishii n. sp.	*Rastrelliger kanagurta*	Red Sea and Arabian Gulf (Saudi Arabia)	6.14±0.38 (5.9–6.34)	5.48±0.32 (5.3–5.7)	4.27±0.38 (4.1–4.42)	2.08±0.29 (1.88–2.28)/ 1.31±0.22 (1.10–1.52)	Present work
K. amamiensis	*Seriola quinqueradiata* (type host), *S. dumerili*, *Caranx sexfasciatus*, *Pempheris ypsilychnus*, *Abudefduf bengalensis*, *A. sexfasciatus*, *A. vaigiensis*, *A. whitleyi*, *Chromis chrysura*, *C. notata*, *Chrysiptera cyanea*	Japan and Australia	5–6 7.77 (6.84–8.24) 7.88 (7.48–8.37)	5–6 6.63 (5.83–7.14) 6.81 (6.47–7.09)	4.5–5 5.03 (4.56–5.85) 5.28 (4.94–5.84)	1.5–2/1–1.2 2.16 (1.83–2.68)/0.44 (1.12–1.76) 2.24 (2.01–2.52)/1.40 (1.13–1.67)	Egusa and Nakajima (1980) Burger et al. (2008)
K. azoni	*Pleurogrammus azonus* *Hexagrammos octogrammus*	Japan	6.2–7.2	5.2–6.0	5.0–6.0	2.0–2.2/1.0–1.5.	Aseeva 2004
K. sebastea	*Sebastes minor*	Japan	7.3–8.2	5.0–5.5	5.4–5.6	2.0–2.2/0.8–1.0	Aseeva 2002
K. scomberi	*Scomber japonicus*		9.2 (8.2–10.5)	8.1 (7.0–8.8)	6.4 (6.1–6.8)	2.9 (2.5–3.4)/1.6 (1.3–2.0)	Li et al. 2013
K. kenti	*Dischistodus perspicillatus*	Australia	(8.4–9.1)	(7–7.6)	(5.1–6.1)	(2–2.2)/(1.6–1.8)	Burger and Adlard, 2010
K. trachuri	*Trachurus japonicus*	Japan	7.9 (7.0–8.5)	5.8 (5.3–6.2)	6.1 (5.5–6.9)	2.9 (2.6–3.5)/ 2.0 (1.6–2.2)	Matsukane et al. 2011
K. crumena	*Scomberomorus maculatus*	South Florida	9.9 (9.3–10.4)	9.0 (8.2–9.7)	7.5 (6.8–8.2)	4.0 (3.2–4.6)/2.5 (2.1–2.9)	Iversen and Van Meter (1967)
K. thunni	*Thunnus alalunga*	Pacific Ocean	9.5 (9.2–9.9)	8.3 (7.7–9.0)	6.5 (6.4–6.6)	2.5 (2.2–2.9)/ 2.1 (1.9–2.2)	Matsukane et al. (2011)
K. shiomitsui	*Thunnus orientalis*/ *Takifugu rubripes*	Japan	9.4±0.31 (8.6–9.8)	7.2±0.27 (6.7–7.5)	6.2±0.36 (5.6–6.8)	2.8±0.2 (2.5–3)/ 1.3±0.11(1–1.4)	Egusa and Shiomitsu 1983; Zhang et al. 2010
K. leptacanthae	*Zoramia* spp.	Australia	8.2±0.52 (6.85–9.03)	7±0.44 (5.9–7.8)	6±0.48 (5.06–7.12)	2.7±0.32 (2.07–3.3)/ 1.3±0.12 (1.04–1.51)	Heiniger and Adlard 2012
K. pagrusi	*Pagrus pagrus*	Red Sea	6.4±0.4 (5.8–7.2)	6.4±0.4 (5.8–7.2)	7±0.8 (6.5–8.6)	3.7±0.3 (2.6–4.2)/1.5±0.2 (1–1.8)	Al–Quraishy et al. 2008
K. nova	*Thynnus obesus*, *Trachurus* spp., *Neogobius* spp., *Gobius* spp., and others	Atlantic Ocean/Black Sea/Mediterranean Sea	5.1–7.7 (6.2)		5.1–7.7 (6.2)	1.3–2.6 (1.8)	Moran et al. 1999; Kovaleva et al. 1979; Campbell 2005
K. clupeidae	*Brevoortia tyrannus* (Clupeidae)	USA East Coast	6.5 (6.5)	5.5–6.5 (6.0)	5.0–5.5 (5.25)	1.3–1.5 (1.4)/1.0 (1.0)	Reimschuessel et al. (2003)

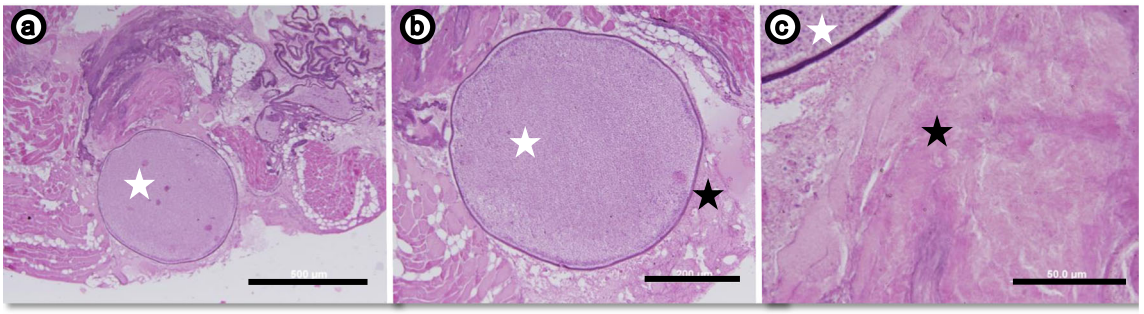

Fig. 3 Stained histological sections of infected muscle of *R. kanagurta* with *K. quraishii*. **a** Pseudocysts (*white asterisks*) surrounded by a thinner fibrous envelope is located between myofibers. **b**, **c** Local myolysis of muscle fibers (*black asterisks*) around the pseudocysts. *Scale bars*: **a** 500 μm; **b**, **c** 200 μm; **d** 50 μm

(Schärer and Vizoso 2003) (Table 2). However, finger-like projections reported in the anterior end of spores of *K. amamiensis* and papillae in the inflated corners were not present in *K. quraishii*. Distribution of pseudocysts in the host shows strict localization in the muscles throughout the body. For *K. amamiensis*, pseudocysts were observed in the striated

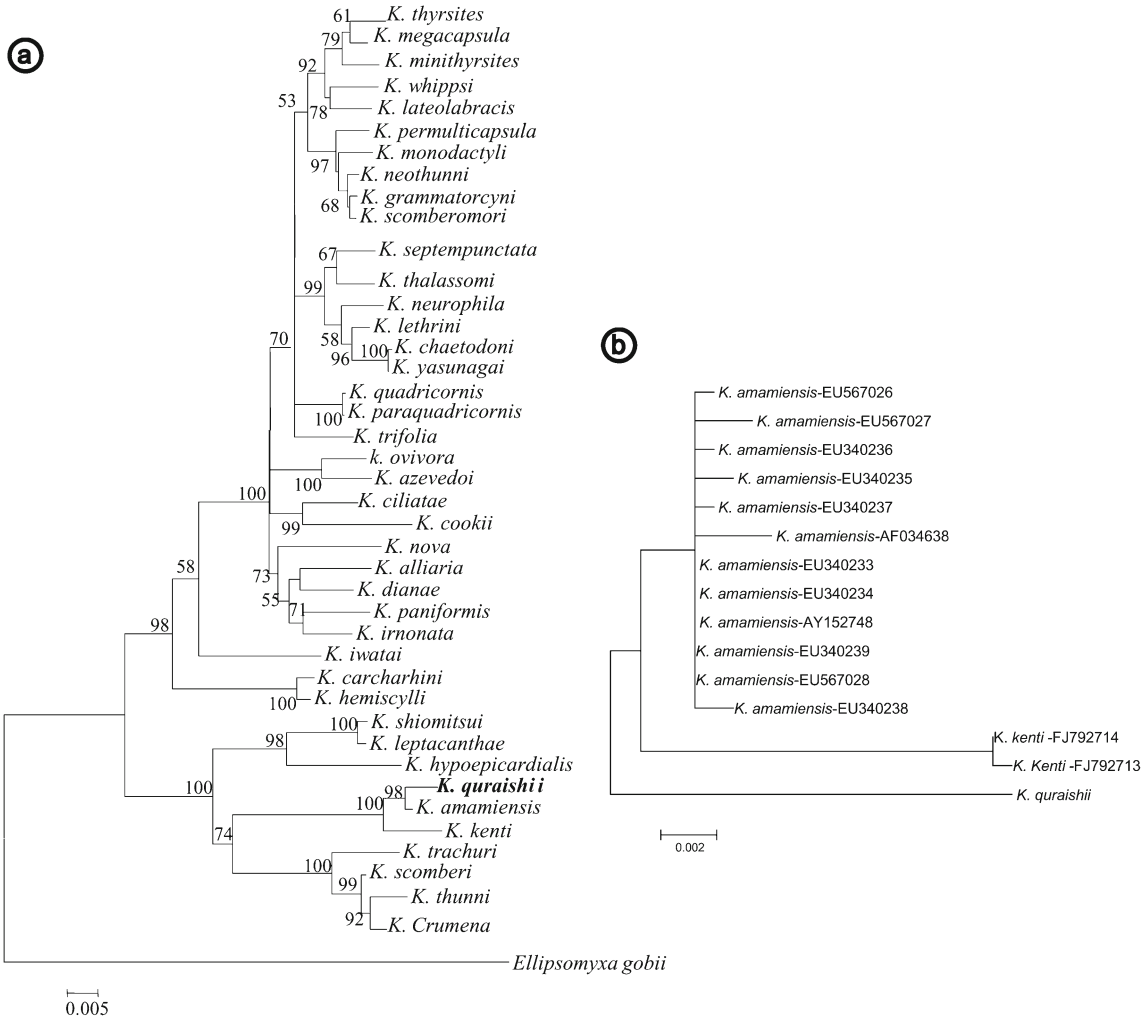

Fig. 4 phylogenetic trees based on analysis of SSU rDNA data. **a** Maximum likelihood tree based on the 18S rDNA sequence. The tree with the highest log likelihood (−8705.2322) is shown. Nodal supports are indicated for maximal likelihood. *Ellipsomyxa gobii* was used us outgroup. **b** Subtree showing the position of *K. quraishii* relative to *K. amamiensis* and *K. kenti* isolates. The trees were drawn to scale, with branch lengths measured in the number of substitutions per site

Table 3 Matrix of percentages of similarity between *Kudoa quraishii*, *K. amamiensis*, and *K. kenti* over 1,518 nucleotide positions

Number	Species and accession number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	*K. amamiensis* AF034638		4 (0/4)	4 (0/4)	4 (0/4)	6 (2/4)	5 (0/5)	5 (1/4)	6 (2/4)	4 (0/4)	5 (1/4)	7 (2/5)	4 (0/4)	24 (15/9)	23 (14/9)	*25 (12/13)*
2	*K. amamiensis* AY152748	99.73		0	0	2 (2/0)	1 (0/1)	1 (0/1)	2 (2/0)	0	1 (1/0)	3 (2/1)	0	20 (15/5)	19 (14/5)	*21 (12/9)*
3	*K. amamiensis* EU340233	99.73	100		0	2 (2/0)	1 (0/1)	1 (0/1)	2 (2/0)	0	1 (1/0)	3 (2/1)	0	20 (15/5)	19 (14/5)	*21 (12/9)*
4	*K. amamiensis* EU340234	99.73	100.00	100.00			1 (0/1)	1 (0/1)	2 (2/0)	0	1 (1/0)	3 (2/1)	0	20 (15/5)	19 (14/5)	*21 (12/9)*
5	*K. amamiensis* EU340235	99.59	99.86	99.86	99.86			3 (2/1)	4 (4/0)	2 (2/0)	3 (3/0)	5 (4/1)	2 (2/0)	22 (17/5)	21 (16/5)	*23 (14/9)*
6	*K. amamiensis* EU340236	99.66	99.93	99.93	99.93	99.79		2 (1/1)	3 (2/1)	1 (0/1)	2 (1/1)	4 (2/2)	1 (0/1)	21 (15/6)	20 (14/6)	*22 (12/10)*
7	*K. amamiensis* EU340237	99.66	99.93	99.93	99.93	99.79	99.86		3 (3/0)	1 (1/0)	2 (2/0)	3 (2/1)	1 (1/0)	21 (16/5)	20 (15/5)	*21 (12/9)*
8	*K. amamiensis* EU340238	99.59	99.86	99.86	99.86	99.73	99.79	99.79		2 (2/0)	3 (3/0)	4 (3/1)	2 (2/0)	22 (17/5)	21 (16/5)	*22 (13/9)*
9	*K. amamiensis* EU340239	99.73	100.00	100.00	100.00	99.86	99.93	99.93	99.86		1 (1/0)	3 (2/1)	0	20 (15/5)	19 (14/5)	*21 (12/9)*
10	*K. amamiensis* EU567026	99.66	99.93	99.93	99.93	99.79	99.86	99.86	99.79	99.93		4 (3/1)	1 (1/0)	21 (16/5)	20 (15/5)	*22 (13/9)*
11	*K. amamiensis* EU567027	99.52	99.79	99.79	99.79	99.66	99.73	99.73	99.66	99.79	99.73		3 (2/1)	23 (17/6)	22 (16/6)	*25 (15/10)*
12	*K. amamiensis* EU567028	99.73	100.00	100.00	100.00	99.86	99.93	99.93	99.86	100.00	99.93	99.79		20 (15/5)	19 (14/5)	*21 (12/9)*
13	*K. kenti* FJ792713	98.19	98.47	98.47	98.47	98.33	98.40	98.40	98.33	98.47	98.40	98.26	98.47		1 (1/0)	*38 (24/14)*
14	*K. kenti* FJ792714	98.26	98.54	98.54	98.54	98.40	98.47	98.47	98.40	98.54	98.47	98.33	98.54	99.93		*39 (25/14)*
15	*K. quraishii KF413764*	*97.98*	*98.26*	*98.26*	*98.26*	*98.12*	*98.19*	*98.19*	*98.26*	*98.26*	*98.19*	*98.05*	*98.26*	*97.13*	*97.20*	

Values related to *K. quraishii* are shown in italics. Lower triangle shows percentage of similarity, and upper triangle shows number of different nucleotides (number of transitions/transversions in parenthesis)

muscles but also in case of heavy infection in the heart, skin, and fins (Schärer and Vizoso 2003; Burger et al. 2008). The size and structure of pseudocysts between the two species are roughly similar. However, in the case of *K. quraishii*, the pseudocysts were surrounded by a very thin layer of fibrous envelope without any inflammatory reaction as reported for other species (Abdel-Ghaffar et al. 2012; Burger et al. 2008). Myolysis is not frequent and localized to the surrounding myofibers.

Molecular analysis, based on partial sequence of SSU rDNA gene, shows strict association of *K. quraishii* with *K. amamiensis* forming together with *K. kenti* a strong cluster supported by bootstrap of 100. This molecular affinity between *K. quraishii* and *K. amamiensis* supports the morphometric similarities between the two species. Comparison of nucleotide sequences between 41 different *Kudoa* species for a total of 1,526 positions shows that the lowest percentage of difference with *K. quraishii* was observed with the sequence of *K. amamiensis* (1.7 %) and *K. kenti* (2.8 %) (Table 1). Differences were between 7.6 and 8.8 % with *K. thunni*, *K. crumena*, *K. scomberi*, *Kudoa hypoepicardilis*, *K. leptacantha*, and *K. shiomitsui*. The differences did not exceed 13 % with the other analyzed *Kudoa* sequences (Table 1). In addition, comparisons between all the deposited *K. amamiens*is sequences from different hosts in Japan and Australia show that the percentage of similarity varies between 98.3 and 98 % (Table 3). However percentage of similarity between *K. amamiensis* sequences was between 99.59 and 100 % and was of 99.93 % between the most isolates. The sequence of *K. kenti* presents 98.47 to 98.19 % with the other *K. amamiensis* sequences. The number of different nucleotides between *K. amamiensis* sequences and *K. quraishii* thorough the analyzed sequences was between 21 and 25 bp with 12 to 15 transitions and 9 to 13 transversions. However, between *K. amamiensis* sequences, these differences vary between 0 and 6 bp. We notice that sequences of *K. kenti* have 19 to 23 bp differences with those of *K. amamiensis* with 14 to 16 transitions and 5 to 9 transversions (Table 3). The two deposited *K. kenti* sequences have 99.93 % of similarity and are different by only 1 transition. Compared to *K. kenti*, *K. quraishii* sequence has 38 to 39 bp difference distributed to 24 or 25 transitions and 14 transversions.

In the light of these structural and molecular data, we can state that the present *Kudoa* reported in the Indian mackerel is a new species different to *K. amamiensis* and *K. kenti*.

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