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First report of adults of *Acanthocephaloides irregularis* from cuttlefish *Sepia officinalis* (Cephalopoda) in Tunisia: SEM observations and molecular analysis

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Abstract: During a parasitological survey of the common cuttlefish *Sepia officinalis* (Linnaeus) collected from the Bizerte Lagoon in northern Tunisia, adult acanthocephalans were found attached to the internal wall of cuttlefish stomach. The presence of adult acanthocephalans in cephalopods is unusual, given that definitive hosts for these obligate endoparasites are typically vertebrates. A detailed morphological examination of both sexes using light and scanning electron microscopy revealed high morphological similarities to *Acanthocephaloides irregularis* Amin, Oğuz, Heckmann, Tepe et Kvach, 2011. A partial sequence of 604 bp of the cytochrome oxidase subunit I (COI) gene was successfully generated. Phylogenetic analysis based on COI gene confirmed the identification, showing that the Tunisian isolate of *A. irregularis* clustered closely to *A. propinquus* (Dujardin, 1845) from *Gobius bucchichii* Steindachner. This study presents the first record of *A. irregularis* in *S. officinalis* in the Mediterranean Sea, offering new insights into its life cycle, host specificity, and ecological significance within benthic food webs. This finding raises important questions about the role of cephalopod hosts in the transmission dynamics of acanthocephalans in marine environments.

Keywords: Acanthocephala, morphology, life cycle, COI, Mediterranean Sea

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Cephalopods are a key component of the food web; their foraging behaviour and diet facilitate the transmission of endoparasites (Nicholas 1967). Furthermore, cephalopods inhabit a wide range of biotopes (benthic to pelagic ecosystems), and their behavioural abilities (solitary, erudite) may enable ectoparasite recruitment in major cephalopod stocks. The two arguments above provide a broad perspective for understanding the wide availability of microhabitats and the ubiquity offered by cephalopods for colonisation by metazoan parasites (Pascual et al. 2019).

Among cephalopods, the cuttlefish *Sepia officinalis* (Linnaeus) is one of the most important coastal fishery resources in the Mediterranean Sea (Belcari et al. 2002). This carnivorous species has a broad dietary spectrum (Messenger 1977), with both juveniles and adults feeding on similar prey, primarily crustaceans, bony fishes, molluscs, polychaetes, and other worms (Castro and Guerra 1990, Pinczon du Sel et al. 2000). *Sepia officinalis* can host parasites from a variety of taxonomic groups, spanning both protozoans and metazoans. Based on parasitological surveys from the Mediterranean and Atlantic, the main parasitic groups include coccidians, ciliates, nematodes, trematodes, cestodes and copepods (Hochberg 1990, Gestal et al. 2019).

Only two species of acanthocephalans have been reported from cephalopods. The presence of acanthocephalans in cephalopods is unusual since adults of this entirely parasitic group typically infect only vertebrate hosts (Nicholas 1967). Gaevskaya (1977) described and figured *Neorhadinorhynchus atlanticus* Gaevskaya et Nigmatulin, 1977 from the stomach of the flying squid *Sthenoteuthis pteropus* (Steenstrup) captured in the south of the Gulf of Guinea in the Atlantic Ocean.

Gaevskaya (1977), Naidenova and Zuev (1978) and Gaevskaya and Nigmatullin 1981 found a second species of unidentified acanthocephalan in the mantle of Atlantic specimens of *S. pteropus.* This was the first observation of acanthocephalans in a cephalopod host. While acanthocephalans have been documented in a wide range of marine hosts (Rauque et al. 2002), their occurrence in cephalopods remains poorly understood.

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Table 1. Morphometric comparisons between populations of *Acanthocephaloides irregularis* Amin, Oğuz, Heckmann, Tepe et Kvach, 2011 from different hosts in the Mediterranean and Black Seas. Measurements are in micrometres unless otherwise stated.

Source	Amin et al. (2011)		Jmii Chine et al. (2018)		Present study	
Locality	Gulf of Odessa (Black Sea)		Bizerte Lagoon (Mediterranean Sea)		Bizerte Lagoon (Mediterranean Sea)	
Host	*Proterorhinus marmoratus*		*Dicentrarchus labrax*		*Sepia officinalis*	
Parasite sex	Male	Female	Male	Female	Male	Female
Trunk length (mm)	1.3–4.05	1.5–4.2	1.5–2.2	2.5–3.8	1.7–2.3	2.3–3.8
Trunk width	200–1.083	225–713	233–286	290–413	360–419	305–470
Proboscis length	125–393	218–364	151–176	156–177	104–165	155–173
Proboscis width	88–177	89–178	34–60	55–86	90–101	71–99
Lemnisci length	395–586	275–706	174–320	250–530	367–610	583–766
Hook rows × hooks per row	12 × 5	12 × 5	12 × 4	12 × 5	12/14 × 5	12/14 × 5
Anterior hooks+ posterior hooks	3 + 2	3 + 2	2–3 + 1–2	3 + 2	3 + 2	3+2
Hook 1 length	24–39	26–39	21–27	18–20	15–22	17–24
Hook 2 length	32–55	39–47	30–39	28–35	22–30	20–27
Hook 3 length	45–59	49–63	–	38–45	32–37	28–34
Spinal hook 4 length	16–22	16–24	12–16	13–17	14–17	12–15
Spinal hook 5 length	14–22	18–24	12–15	13–16	10–13	9–14
Anterior testis length	83–375	–	167–176	–	261–320	–
Anterior testis width	66–284	–	67–130	–	277–293	–
Posterior testis length	91–541	–	158–173	–	315–545	–
Posterior testis width	58–263	–	77–170	–	269–328	–
Egg length	–	48–60 × 12–14	–	44–49 × 12–16	–	58– 69

The aim of this work is to characterise adults of *Acanthocephaloides irregularis* Amin, Oğuz, Heckmann, Tepe et Kvach, 2011 infecting *S. officinalis* collected in Tunisia, using light and scanning electron microscopies. Moreover, we used molecular data to confirm species identification and access phylogenetic relationships of *A. irregularis* with other acanthocephalans.

MATERIALS AND METHODS

Cuttlefish and parasite sampling

Between January 2024 and April 2024, a total of 57 specimens of common cuttlefish *Sepia officinalis* ranging between 7.0 to 18.5 cm in length were collected from Bizerte Lagoon situated in north-eastern Tunisia (37.1967N, 9.8564E). The cuttlefish were dissected and examined under a stereomicroscope for the presence of endoparasites. The collected acanthocephalans (11 specimens) were initially placed in saline solution. Subsequently, some were preserved in 70% ethanol for light and scanning electron microscopy (LM and SEM) studies, while others were stored in 100% ethanol for molecular analyses.

Morphological examination

One male and one female specimen were placed in a glycerol solution to observe the details of the proboscis and internal structures. Eleven additional specimens were stained with iron acetocarmine, destained in 1% hydrochloric acid in 70% ethanol, dehydrated through a graded ethanol series (70%–100%), cleared in 98% dimethyl phthalate, and mounted in Canada balsam. All measurements in morphological description are in micrometres (µm) unless otherwise indicated.

Scanning electron microscopy (SEM)

Two females and one male were dehydrated through a graded ethanol series (70%, 90% and 100%), then dried using CO_2 in an Emitech K850 critical point dryer. The specimens were mounted, coated with palladium using a Quorum Technologies SC7640 sputter coater, and examined with a Hitachi S-3400N scanning electron microscope at an accelerating voltage of 10 kV at the University of Corsica Pascal Paoli (Corte, France).

Molecular and phylogenetic analyses

One specimen was used for molecular analysis. Total genomic DNA was extracted using the QIAamp DNA Mini Tissue Kit (Qiagen, Germany), following the manufacturer's recommendations. The quantity and quality (purity) of extracted genomic DNA was assessed using a NanoDrop 8000 (Thermo Scientific™). The amplification of partial cytochrome oxidase subunit 1 (COI) DNA fragment was conducted through PCR using COI-F (5′-AGTTCTAATCATAARGATATYGG-3′) and COI-R (5′-TAAACT-TCAGGGTGACCAAAAAATCA-3′) primers (Folmer et al. 1994).

For each PCR reaction, 30 µl final volume was used, containing 15 µl of 2X DreamTaq PCR Master Mixes (Thermofisher, UK), 2 µl (100 ng) genomic DNA, 1.5 µM forward and reverse primers and 10 µl DNAse/RNAse free water. The PCR reactions were performed in the thermocycler apparatus T100™ (Bio-Rad, US) in the Zoology Department, King Saud University. The quality of the PCR products was assessed on agarose gel electrophoresis and visualised with UV transluminator. The PCR product was then sequenced in both directions using the same PCR primers with ABI 3130 sequencer. The sequences were visually checked and manually edited with Chromas software 2.6.6 (Technelysium Pty Ltd., Brisbane, Queensland, Australia). Similar sequences were obtained using BLASTn (blast.ncbi.nlm.nih.gov) (Altschul et al. 1997) and used for phylogenetic analysis. Multiple sequence alignments were conducted with ClustaX software (Thompson et al. 1997).

Phylogenetic relationships between related acanthocephalans were inferred with Bayesian inference (BI) and maximum likelihood (ML) methods. BI analysis was performed in MrBayes version 3.2.6 (Ronquist et al. 2012) using Markov Chain Monte Carlo (MCMC) for 2,000,000 generations with two independent runs of four simultaneous MCMC chains (nchains = 4). Trees were saved every 100 generations (samplefreq = 100). A 25% burn-in (default setting) was applied. ML analysis was performed using the PhyML v3.0 online execution program (Guindon et al. 2010)

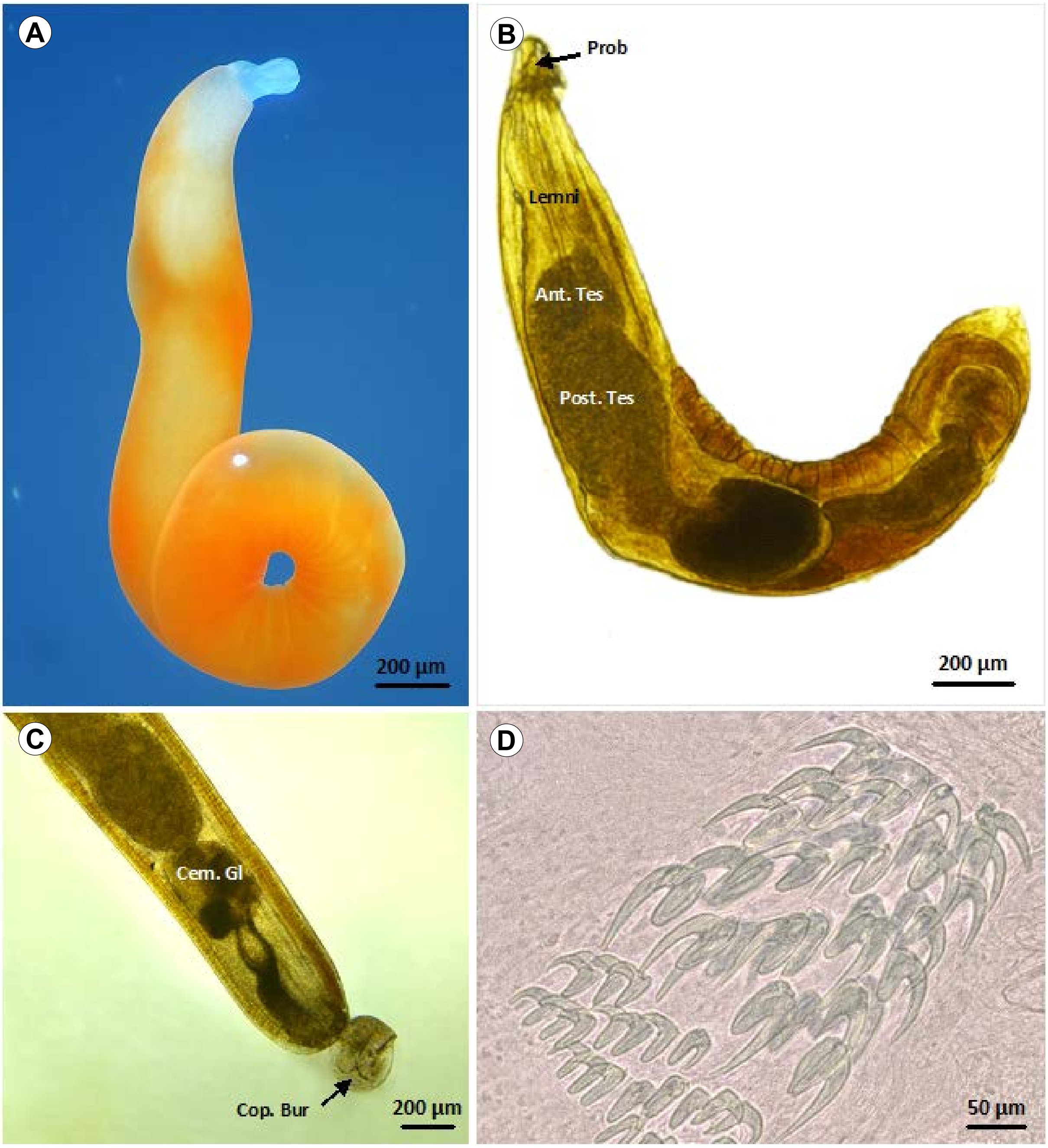

Fig. 1. Light microscopy of a male body of *Acanthocephaloides irregularis* Amin, Oğuz, Heckmann, Tepe et Kvach, 2011 from *Sepia officinalis* (Linnaeus) in Tunisia. **A**, **B** – male; total view; **C** – posterior trunk; **D** – proboscis. *Abbreviations*: Ant. Tes – anterior testis; Cem. Gl – cement gland; Cop. Bur – copulatory bursa; Lemni – lemniscus; Post. Tes – posterior testis; Prob – proboscis.

using the GTR + I + G model, as selected by evaluation with jModelTest 2.1.10 (Darriba et al. 2012). The reliability of the tree was supported with Bootstrap value based on 1,000 replications.

RESULTS

Morphological description

Family Arhythmacanthidae, Yamaguti, 1935

Acanthocephaloides irregularis Amin, Oğuz, Heckmann, Tepe et Kvach, 2011 (Figs. 1–3)

Description

Aryhtmacanthidae with characters of the genus *Acanthocephaloides* Meyer, 1932. Body quite small, fusiform, slightly swollen in median part (Figs. 1A, 2A). Females larger than males (Table 1). Trunk entirely covered with small spines (seen only with SEM) (Fig. 2F,G). Trunk pores present (Fig. 2C). Trunk spines randomly distributed, most dense anteriorly, pointed posteriorly (Fig. 2A,F,G). Genital spines directed anteriorly (Fig. 2F). Proboscis cylindrical, short, with 12–14 longitudinal rows of 5 hooks: apical, subapical and median blunt-ended hooks increasing in size progressively posteriorly, followed by 2 (rarely 3) small, equally long, spiniform hooks (Figs. 1D, 2B,D,E).

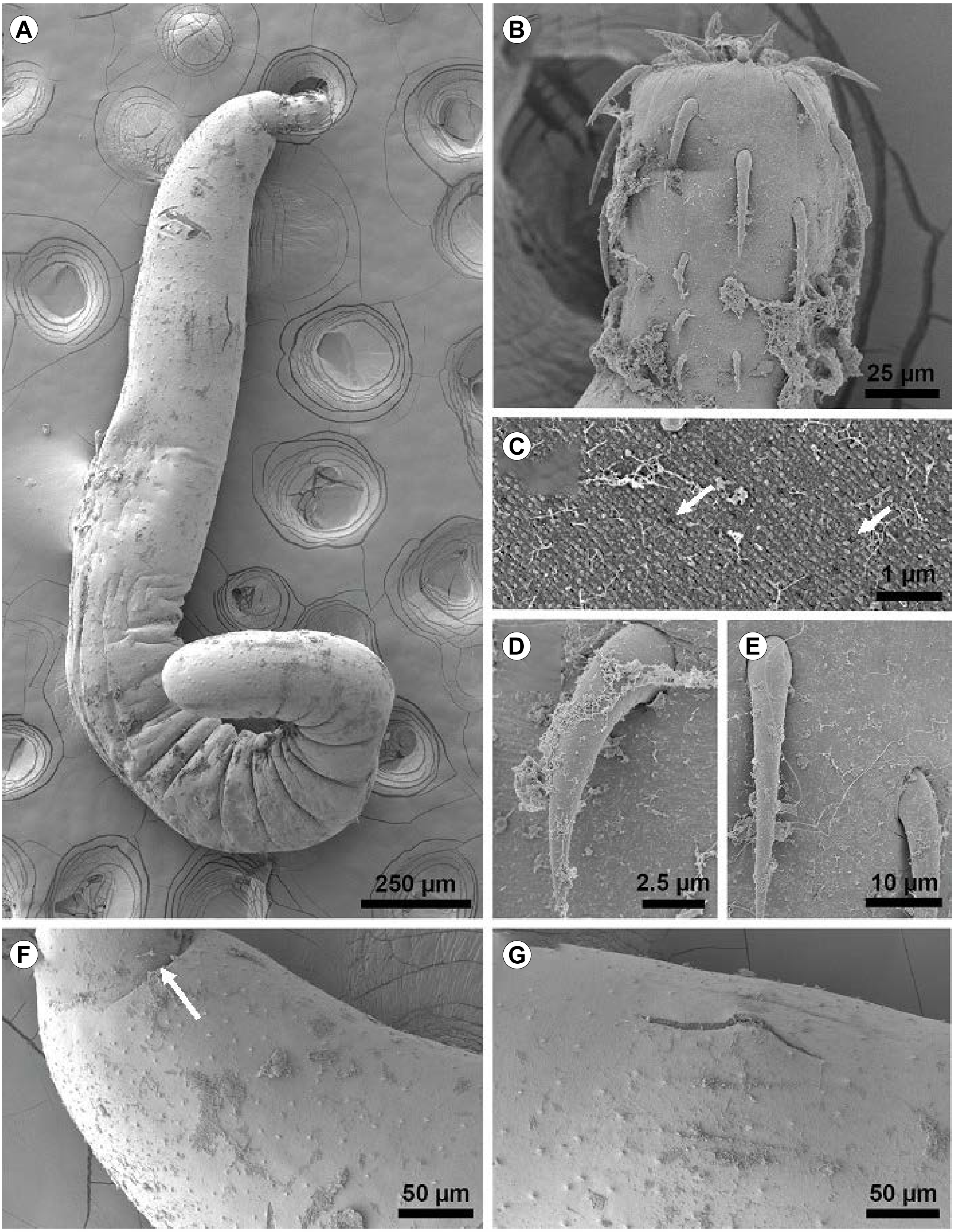

Fig. 2. SEM micrographs of the female of *Acanthocephaloides irregularis* Amin, Oğuz, Heckmann, Tepe et Kvach, 2011 from *Sepia officinalis* (Linnaeus) in Tunisia. **A** – female total view, showing the elongate trunk and anterior collar. **B** – proboscis, showing its cylindrical form with a median swelling; note the alternating position of the hooks and spines in each circle. **C** – anterior body trunk showing pores (white arrows). **D** – a spiniform hook on pthe roboscis. **E** – detailed blunt proboscis hook. **F** – terminal gonopore of a female specimen, showing its lateral orientation (arrow). **G** – anterior spines on the female trunk oriented posteriorly.

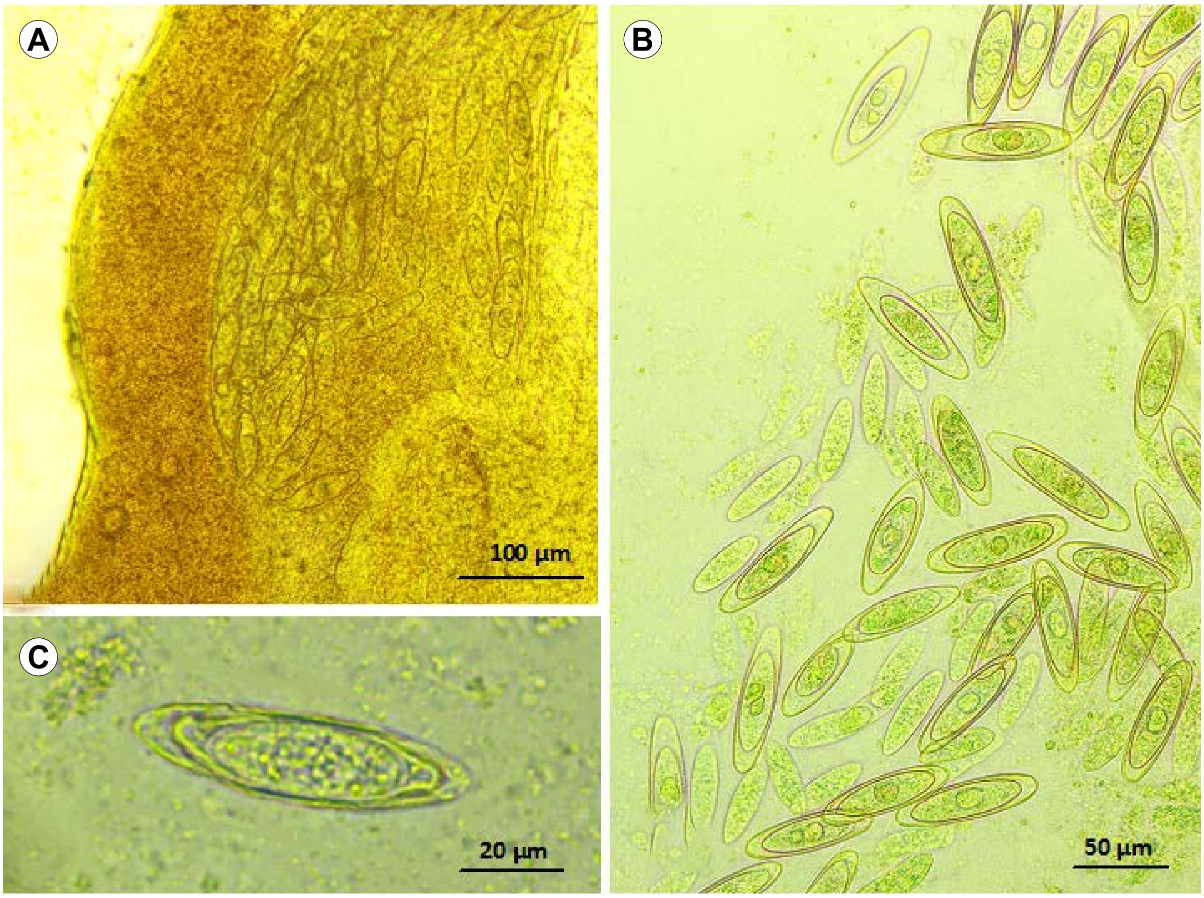

Fig. 3. Eggs of female of *Acanthocephaloides irregularis.* **A** – portion of the uterus filled with eggs; **B** – free eggs; **C** – fusiform egg showing polar prolongation of fertilisation membrane.

Each of apical, subapical and median hook circles alternating in position and size (Figs. 1D, 2D). Apical hooks forming circle of small hooks with pointed end (Fig. 2B). Hooks on proboscis gradually decreasing in size posteriorly. Proboscis hook and spine roots with anterior manubria (Fig. 1D). Cephalic ganglion present at base of receptacle. Nucleated pouches at posterior end of receptacle were observed on alive specimens. Neck short, unarmed. Receptacle double-walled. Lemnisci elongated, roughly equal in size, digitiform and longer than receptacle. Lemnisci touching anterior testis in folded trunk (Fig. 1B).

Male (based on eight males; measurements in Table 1). Two ovoid testes in tandem. Anterior testis almost rounded, slightly smaller than posterior testis (Fig. 1B,C). Cement glands 6, pyriform, with 2 cement gland ducts (Fig. 1C). Genital orifice terminal. Prominent sensory discs not observed on copulatory bursa.

Female (based on two gravid females; measurements in Table 1). Body fusiform. Gonopore subterminal. Uterus relatively long. Eggs spindle-shaped, with polar prolongation of fertilisation membrane (Fig. 3).

Taxonomic summary

Host: *Sepia officinalis* (Linnaeus) (Cephalopoda: Sepiidae), common cuttlefish.

Locality: Bizerte Lagoon, northern Tunisia.

Site of infection: Stomach.

Voucher material: deposited in the collections of the Museum National d'Histoire Naturelle (MNHN-IN-129YT), Paris, France (two males and one female on one slide).

Representative DNA sequences: The COI sequence of *A. irregularis* was deposited in the GenBank database under the accession number PX640512 .

Prevalence and intensity: Two out of 57 cuttlefish (prevalence 4%) were infected with acanthocephalans, yielding a total of 11 worms. The first infected specimen harboured six worms and the second specimen harboured five worms.

Molecular and phylogenetic analyses

A partial sequence of 604 bp of the mitochondrial cytochrome c oxidase subunit I (COI) was successfully obtained from *A. irregularis* and deposited in GenBank under accession number (PX640512). BLASTn analysis revealed a relatively low sequence similarity with available sequences in GenBank. The highest similarity (85.5%) was obtained with *Acanthocephaloides propinquus* (Dujardin, 1845) (GenBank accession DQ089713) generated by García-Varela and Nadler (2006). The similarity with all other acanthocephalan taxa was <75%, indicating a marked genetic distinctness of the Tunisian specimens. To our knowledge, this represents the first COI sequence of *A. irregularis*.

Phylogenetic trees constructed using both maximum likelihood (ML) and Bayesian inference (BI) methods yielded

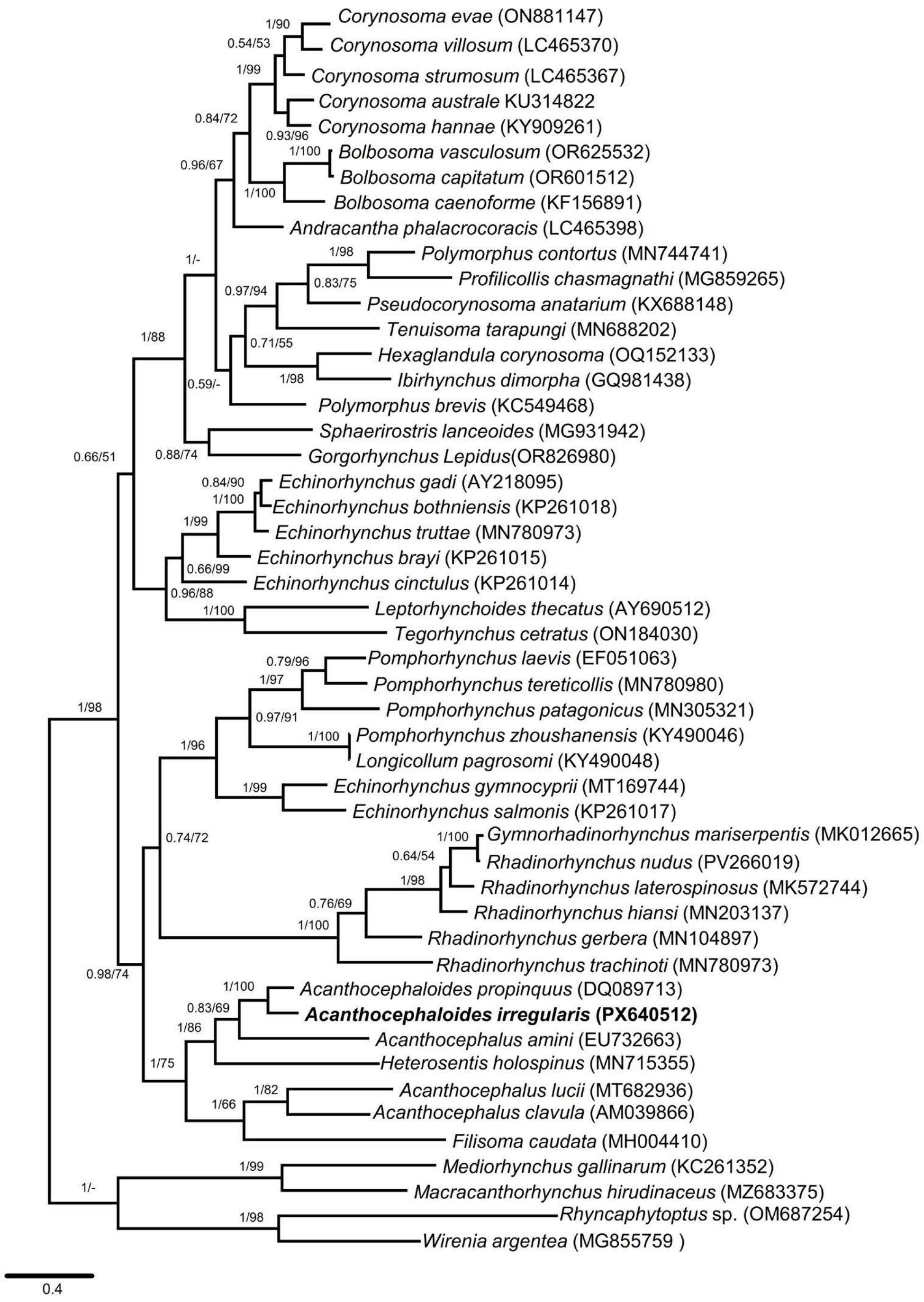

Fig. 4. Bayesian inference (BI) phylogenetic tree based on partial mitochondrial *cytochrome c oxidase subunit I* (COI) gene sequences of acanthocephalan taxa. The analysis shows *Acanthocephaloides irregularis* Amin, Oğuz, Heckmann, Tepe et Kvach, 2011 clustering with *Acanthocephaloides propinquus* (Dujardin, 1845) (GenBank accession DQ089713) with strong nodal support (BI posterior probability = 1.00; ML bootstrap = 100%). Numbers at the nodes indicate posterior probabilities (left) and maximum-likelihood bootstrap values (right). The scale bar indicates the number of substitutions per site. All comparative sequences were retrieved from GenBank, and their accession numbers are provided after species names.

congruent topologies (Fig. 4). Both analyses recovered a well-supported clade (BI posterior probability = 1.00; ML bootstrap = 100%) comprising *A. irregularis* and *A. propinquus*, confirming their close relationship within the family Arhythmacanthidae. This *Acanthocephaloides* clade was positioned among other acanthocephalans such as those of the families Echinorhynchidae and Pomphorhynchidae, consistent with previous molecular classifications of the group (García-Varela and Nadler 2006, Amin et al. 2011).

DISCUSSION

Several morphological features observed in the collected acanthocephalans confirm their identification as *Acanthocephaloides irregularis*. This species was originally described by Amin et al. (2011) from four marine fish hosts, belonging to the families Blenniidae, Gobiidae and Syngnathidae from the Gulf of Odessa in Ukraine. The close similarity in measurements and counts of morphometric characters of our specimens is consistent with their assignment to this acanthocephalan species. Characters like the presence of a nuclear pouch at the base of the receptacle and the irregular distribution of trunk spines, which are specific to *A. irregularis*, are observed in our specimens.

Compared to the original description, the acanthocephalan found here presents a proboscis armature similar to that of specimens found in the Black Sea (Amin et al. 2011). Moreover, *A. irregularis* has been previously reported in the European sea bass, *Dicentrarchus labrax* (Linnaeus) (Moronidae) in the same sampling location as our study (Bizerte Lagoon) by Jmii Chine et al. (2018). Adults of acanthocephalans found in the present work infecting the stomach of the common cuttlefish were similar to those found in *D. labrax* and differed from the specimens found in the Black Sea, particularly in the absence of a trunk collar and the subterminal position of the gonopore. Nevertheless, no pores were detected on the trunk spines in our specimens, in contrast to the descriptions provided by Amin et al. (2011) and Jmii Chine et al. (2018). *Acanthocephaloides irregularis* found in the present study closely resembles *Acanthocephaloides propinquus* 3, which has been found in various teleost fish species in both the Mediterranean and Black Seas (Kvach 2006, Oğuz and Kvach 2006, Gargouri et al. 2016).

In addition, the present study provides the first molecular data for *A. irregularis*, thereby filling a significant gap in the molecular taxonomy of the genus *Acanthocephaloides*. The generated COI sequence revealed sequence divergence (~14.5%) between *A. irregularis* and *A. propinquus* (DQ089713), which is well above the usual intraspecific COI variation. This indicates a high level of genetic divergence, confirming that the present specimens represent a genetically distinct lineage within *Acanthocephaloides*.

The phylogenetic analyses placed *A. irregularis* within a well-supported *Acanthocephaloides* clade, forming a sister relationship with *A. propinquus*, thereby confirming their close evolutionary affinity. This genetic differentiation, coupled with the morphological distinctiveness noted above, supports the recognition of *A. irregularis* as a valid and distinct species.

The unusual occurrence of *A. irregularis* in the cephalopod *Sepia officinalis* suggests multiple possible interpretations. Several parasitological studies have shown that cephalopods can serve as intermediate, paratenic or definitive hosts for a wide range of parasitic species with diverse life cycle strategies (Hochberg 1990, Gestal et al. 2019). Parasites can be found in multiple niches and sites in their host and exhibit complex associations in cephalopods (Hochberg 1990, Pascual et al. 1996, Souidenne et al. 2016).

Reports of adult acanthocephalans in invertebrates are rare. To the best of our knowledge, the only known species of an adult acanthocephalan in cephalopods, specifically in squids, was found in the Atlantic Ocean, southern Gulf of Guinea. Gaevskaya and Nigmatullin (1977), has found a cavisomid species, *Neorhadinorhynchus atlanticus,* attached to the stomach of the flying squid *Sthenoteuthis pteropus*. A detailed morphological description of gravid females was provided by the authors. This finding was confirmed by other studies made on the same cephalopod in the central and northern Atlantic, where similar forms of the acanthocephalan were observed (Naidenova and Zuev 1978, Hochberg 1983). The authors proposed that the cephalopod might function as a final host in this case and not simply a paratenic or transfer host (Hochberg 1983).

These previously reported results and the present case could be explained by a parasite adaptation to a new definitive host, which may result from changes in definitive host availability. When a definitive host species becomes scarce, the parasite may switch to a more abundant, but previously less suitable, host. One of the concepts that might explain the change of definitive host is the complexity of life cycle. In fact, acanthocephalans exhibit intricate life cycles that commonly require an arthropod intermediate host and a vertebrate definitive host, and in some cases an additional host (Kennedy 2006).

In cephalopods – particularly cuttlefish – the likelihood of acquiring infection is high due to frequent predation on infected intermediate or paratenic hosts, thereby facilitating trophic transmission of parasites. Cephalopods are widely known for their diverse diet and carnivorous behaviour. In Tunisian waters, the common cuttlefish, *S. officinalis*, primarily feeds on crustaceans, fish and even on other cephalopods. A previous study in the Gulf of Tunis, Tunisia, indicated that decapod crustaceans, such as prawns and crabs and fish are the most frequently consumed prey items by *S. officinalis* (Najai and Ktari 1974).

Moreover, one of the factors that mostly influences parasite host switch is environmental changes. Specifically, pollution and habitat alteration that disrupt host-parasite relationships and increase the likelihood of the parasite host switch. Numerous instances of host range expansion, culminating in host switching to phylogenetically unrelated species, have been documented over evolutionary timescales.

One of the rarest examples of studies documents a host-switching event involving the marine acanthocephalan *Corynosoma australe* Johnston, 1937, typically specific to pinnipeds, which was found reproducing in Magellanic penguins *Spheniscus magellanicus* (Forster, 1781) in Brazil. The study may reflect either adaptive colonisation via rare mutations or ecological fitting, as ancestral *Corynosoma* Lühe, 1904 likely infected aquatic birds (Hernández-Orts et al. 2017). This study confirms the idea that trophically transmitted parasites frequently encounter potential new hosts via food web interactions. In the present study, finding 11 alive adults of *A. irregularis* in *S. officinalis* may be explained by the possibility of an unusual temporary host switch from a fish to a carnivorous cephalopod, whereby the parasite exploits the host for reproduction and full life cycle development.

Moreover, many studies carried out on acanthocephalans proved that adults of this group of parasites, which can be firmly attached to their host's intestines, are able to be transmitted and survive in other hosts and can even occupy the same site of attachment (Kennedy 1999). Individuals can grow and attain full sexual maturity in the "new host"; this phenomenon is referred to as postcyclic transmission according to Nickol (1985), Kennedy (1999) and Lassiere and

Crompton (1988). Laboratory experiments proved that acanthocephalan parasites, *Echinorhynchus salmonis* Müller, 1784, transmitted postcyclically could survive for up to 12 weeks in the new host (Hnath 1969). Another study proved that an acanthocephalan belonging to the species *Acanthocephalus tumescens* (von Linstow, 1896) survived for four weeks, increasing in length, and females reached full sexual maturity after their transmission from the common galaxias *Galaxias maculatus* (Jenyns) to rainbow trout *Oncorhynchus mykiss* (Walbaum) (Rauque et al. 2002).

All previously cited experimental results emphasise the fact that acanthocephalans may undergo host shifts as an adaptive strategy, enabling them to exploit alternative hosts in response to environmental changes and thereby ensure their survival. In the context of the present study, cuttlefish can act as reservoirs through their indirect involvement in acanthocephalans' life cycle. However, this remains inconclusive and warrants additional investigations. Further studies will allow a better understanding of complex host-acanthocephalan parasite interactions.

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Author contribution. Souad Ben Jemaa: collected and dissected *Sepia officinalis* individuals, prepared and examined the acanthocephalan specimens. Halima Jmii Chine: examined the acanthocephalans morphologically. Lamjed Mansour: conducted the molecular phylogenetic study of the acanthocephalans. Yann Quilichini: performed the SEM imaging. Sihem Bahri: reviewed and supervised this study. All authors contributed to the writing of this manuscript. All authors checked and edited this manuscript.

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