

ACANTHOCEPHALA AND ITS RELATIONSHIP WITH HELMINTHES AND ROTIFERS: A REVIEW

Monika Panchani*

Department of Zoology, SVP Cluster University, Mandi, India

Article History: Received 12th March, 2021; Accepted 26th March, 2021; Published 2nd April, 2021

ABSTRACT

Many parasitic forms of helminthes inhabit the different animal hosts. Most of them are placed in classes Platyhelminthes, Cestodes and Nematodes. There are some other parasitic forms which show resemblances with helminthes but are placed in different phylum. One of the groups of parasitic worms belongs to phylum *Acanthocephala*. These are thorny-headed or spiny-headed worms, characterized by the presence of an eversible proboscis armed with spines. Phylum *Acanthocephala* includes large number of parasitic worms inhabiting the intestine of different vertebrates ranging from fish to mammals. They live as adults in the intestine of vertebrates and as larvae in arthropods. The most typical forms are *Acanthocephalus*, *Neoechinorhynchus* and *Gigantorhynchus*. Earlier the *Acanthocephala* were thought to be a discrete phylum but recent genome analysis has shown that they are descended from rotifers. This unified taxon is known as Syndermata. As *Acanthocephalans* share characters with Helminthes and with Rotifers, so they are potential model system from the point of evolution of parasitism. In this paper the general characters and life cycle and evolution of *Acanthocephalan* were studied and its relationship with Cestodes, Nematodes and Rotifers were reviewed.

Keywords: Parasitic forms, Helminthes, *Acanthocephala*, Thorny-headed, Evolution *Acanthocephalus*, *Neoechinorhynchus*, *Gigantorhynchus* and *Rotifera*.

INTRODUCTION

The *Acanthocephalans* are endoparasitic worms of intestine. They live as adults in the vertebrate's small intestine and have an indirect life cycle, which utilizes an arthropod as intermediate host. Rudolphi (1802) was the first to name these worms *Acanthocephala* and gave them an ordinal rank, with one genus, *Echinorhynchus* which is the chief genus of *Acanthocephala*. The most typical forms are *Acanthocephalus*, *Neoechinorhynchus* and *Gigantorhynchus*. Van Cleave is known as the "father" of *Acanthocephala* taxonomy in the US. The *Acanthocephala* resemble with the Platyhelminthes and with Cestodes in many characters. Some of characters show similarity with Rotifers. Several authors have placed *Acanthocephala* as a sister group to individual classes within Rotifera based on morphological characters (Lorenzen et al., 1985; Ahlrichs et al., 1995). Molecular phylogenetic studies employing ribosomal genes support this argument (Garey et al., 1996a; Garey et al., 1998). The position of *Acanthocephala*, however, has remained uncertain. Zoologists placed the *Acanthocephala* either with *Platyhelminthes* or with *Aschelminthes*. At present the phylum *Acanthocephala* is divided into three major classes namely *Archiacanthocephala*, *Eocanthocephala* and *Palaeacanthocephala*. Some of the more recent regional

contributions to *acanthocephalan* taxonomy include those by Amin (2000), Salgado-Maldonado (2006), Bhattacharya (2007) and Salgado-Maldonado and Amin (2009).

METHODOLOGY

Several papers were searched and thoroughly studied to analyze the critical description of *Acanthocephalan* and their affinities with Helminthes and Rotifers.

DISCUSSION

In discussion introduction, general characters, life cycle and evolution and affinity with other phylum are discussed.

General characters

They live as adults in the intestine of vertebrates and as larvae in arthropods. The name of the phylum refers to the thorny retractable proboscis that anchors the adult worm to the intestine of the vertebrate host. In addition to the thorny proboscis, *acanthocephalans* are distinguished morphologically as cylindrical and unsegmented worms. In connection with the proboscis apparatus the epidermis forms two elongated bodies termed lemnisci that hang down into the trunk. The trunk is a hollow structure that contains the excretory, reproductive and nervous systems and is

filled with *pseudocoelomic* fluid (Dunagan et al., 1991). *Acanthocephalans* also vary greatly in size and appearance; they may be less than 1 mm long to over 1 m long. The body wall consists of cuticle, syncytial epidermis with spaces and sub-epidermal musculature. *Acanthocephalans* are remarkably adapted to a symbiotrophic lifestyle in that they lack circulatory, respiratory, and digestive systems. The absorption of nutrients occurs entirely through the body wall and is facilitated by a syncytial epidermis and a lacunar system of circulatory channels (Starling, 1985). Respiration is facilitated by simple diffusion. Excretion is usually by diffusion or is rarely facilitated by ciliated flame cells called *protonephridia*, like those in flatworms, connected to excretory tubules. The number of flame bulbs in each protonephridium ranges from about 250 to 700. Like all *pseudocoelomates*, the body cavity lacks a peritoneum. The nervous system is simple, consisting of an anteriorly located mass of neural tissue known as the cerebral ganglion, from which nerves extend. It consists of a central fibrous mass containing ganglion cells, 86 in *Macracanthorhynchus*, 80 in *Hamanniella* and 73 in *Bolbosoma*. A small genital ganglion is associated with the male reproductive system near the posterior end of the body. Special sense organs are not developed as these are endoparasites. It comprises three in the proboscis and several in the male bursa and penis. In the proboscis there is a sensory organ in the center of the tip and in some genera one on each side in the neck. One of the peculiar features is presence of ligament sacs which are hollow tubes of connective tissue with or without accompanying muscle fibers that run the length of the body enclosing the reproductive organs. In the female there are two ligament sacs, a dorsal and a ventral. In males there is only one sac, the ventral sac is absent. The dorsal sac encloses the testes and the cement glands and posteriorly becomes continuous with the genital sheath. There is presence of pseudocoel a cavity without lining membrane filled with a clear fluid, between the body wall and the ligaments. The reproductive organs occupy the greater part of the body. The sexes are separate and the female is larger than the male. In both the sexes the gonads and their ducts are connected with a ligament strand which extends backwards from the end of the proboscis sheath. In males there are two oval, rounded or elongated testes enclosed in the ligament sac and attached to the ligament strand. From each testis a sperm duct proceeds posteriorly inside the ligament sac. Small enlargements representing spermiducal vesicles may occur along the sperm ducts. A cluster of unicellular gland cells known as cement glands open into the sperm duct behind the posterior testis. These are usually six or eight in number and of variable shape-rounded, pyriform or tubular. The ducts of these cement glands, either separately or after union into one or two main ducts, enter the common sperm duct. The sperm ducts, the cement ducts and the protonephridial canals (when present) are all enclosed in a muscular tube, the genital sheath. The genital sheath terminates on the muscle cap of bursa. Inside the genital sheath, the two sperm ducts unite to a common sperm duct which may present a saccular enlargement, the seminal vesicle, the cement duct enter the common sperm duct and the common protonephridial canal,

when present, also unites with common sperm duct. The urogenital canal so formed penetrates the center of the penis, In female reproductive system departs from the usual in many ways. The original single or double ovary breaks up into fragments termed ovarian walls that float free in the dorsal ligament sac but as the latter sac soon ruptures the balls occupy the pseudocoel. The ligament sacs lead to the first part of the female canal termed the uterine bell which is muscular, funnel- shaped or tubular organ. At its posterior end the bell narrows to a uterine tube composed of several large cells with conspicuous nuclei and bearing two bell pouches that extend anteriorly. The uterine tube enters the uterus a muscular tube of some length and this is followed by the short non-muscular vagina opening to the exterior. The nephridia lie alongside the uterine bell, the two protonephridial ducts run in the dorsal wall of the bell and the common canal formed by their union opens into the beginning of the uterine tube.

Life cycle

Life cycle is completed through the two hosts; larval stage completed through arthropods and adults within the intestine of vertebrates. *Acanthocephalans* are obligately sexual with a life cycle that alternates between arthropod and vertebrate hosts (Crompton et al., 1985; Schmidt et al., 1985; Dunagan et al., 1991). The type of arthropod intermediate hosts used by each *acanthocephalan* class is conservative and hence diagnostic. *Archiacanthocephala* utilize myriapods and insects, *Palaeanacanthocephala* utilize *malacostracans*, and *Eoacanthocephala* utilize *maxillopods* (Bullock et al., 1969; Schmidt et al., 1985; Near et al., 1998). *Acanthocephalans* are *gonochoristic* and invariably utilize arthropods as intermediate hosts and vertebrates as definitive hosts. Occasionally, vertebrates serve as paratenic hosts harboring larval *acanthocephalans* that do not develop to adults unless ingested by the appropriate vertebrate definitive hosts (Nickol et al., 1985). The early advanced phase of development takes place in the pseudocoel. The embryo is encased within a sac and the anterior end is provided with hooks. This stage is called *acanthor* stage. The *acanthor* larva contains a hooked rostellum that is used in penetrating host's tissue. At this stage the embryo is extruded from the intestine of the host along with the faeces. Further development is only possible if the embryo is swallowed by an intermediate host. The intermediate host in all the forms is some Arthropods. After reaching into the intestine of the intermediate host, the chitinous membranes dissolve and the embryo undergoes further development. The embryo either remains fixed to the intestinal wall or migrates into the body cavity. If the intermediate host is taken by the permanent host, attainment of adult size and sexual maturity are achieved. In *Platyhelminthes* life cycle is digenetic means completes its life cycle in two hosts. Larval stages are sporocyst, redia, miracidium, cercaria, metacercaria, coracidium, plerocercoid etc. in cestodes it forms hexacanth, onchoshere, cysticercus and cystacanth larva in intermediate hosts. in nematodes larval forms are rhabditiform and filariform and microfilaria. Both the Nematoda and Platyhelminthes contain obligate parasites

as well as free-living species. Comparison of parasitic and free-living species in these groups is complicated by the very large diversity of species in each of these lineages and the difficulties associated with developing phylogenetic hypothesis for such large groups of organisms.

Evolution and affinities of *Acanthocephala*

Acanthocephalans are regarded as potential model system to study the adaptive processes associated with the evolution of parasitism. *Acanthocephala* resemble with the Platyhelminthes, Cestodes and Rotifers in the many respects. Cholodkovsky (1897) was the first to propose such a relationship since Leuckart's early accounts; this view was supported by Skrjabin and Shults (1931) and Petrochenko (1952). The similarities and dissimilarities between the three groups have also been done (Van Cleave, 1941; Amin et al. 2009). *Platyhelminthes* characters such as presence of armed and protrusible proboscis occurs in certain cestodes, the shape and arrangement of hooks in *Trypanorhyncha* and *Acanthocephala* is similar. Presence of cuticle and syncytial nucleated epidermis. Presence of with circular as well as longitudinal fibers in musculature. Excretory organs are *Protonephridia* of flame-bulbs. Reproductive system, particularly in male, resembles that of many flatworms. Embryology is like that of Cestodes. Serological tests indicate a relationship of *Acanthocephala* with Cestodes rather than nematodes. Because of the absence of gut in acanthocephalans and tapeworms, both groups have also been considered related. Traditionally acanthocephalans were considered to be related to a number of *pseudocoelomate* animal phyla in the *Aschelminthes* (Hyman et al., 1951; Brusca et al., 1990). *Acanthocephala* also shows similarities with *Aschelminthes* such as the division of the body into the presoma and the trunk as in *priapulids* and the *gordiacean* larva. An armed proboscis is found among the *Aschelminthes* in *echinoderids*, *priapulids* and *gordiacean* larva. *Acanthocephala*, however, differs from the Nematoda in presence of proboscis, absence of digestive tract, presence of circular muscles, presence of ciliated excretory organs and complexities of reproductive system. The general structure is rather on the *aschelminthic* side, whereas the embryology presents more points of resemblance with the *Platyhelminth*. Superficial segmentation, sometimes involving musculature, is also conspicuous in rotifers, *echinoderids*, *priapulids* and nematodes, etc. Presence of cuticle and syncytial nucleated epidermis. Division of pseudocoel by partitions and tissues resembling mesenteries. Reduction of gut to a strand is found in male Rotifers. Excretory organs are Flame-bulb *protonephridia*. A close relationship of nephridial and reproductive systems is common in *priapulids* and Rotifers. The Rotifera is a phylum of 2000 species, generally aquatic and free-living, unified by the possession of the corona (an apical, ciliated region surrounding the mouth used for locomotion and food gathering) and the mastax (a muscular pharynx with hard parts used to process food). The phyla *Acanthocephala* and Rotifera occupy a basal position among the triploblast protostomes. For this clade the name *Syndermata* was suggested by Alrichs (1997).

The *acanthocephalan* has long been regarded as unique

and deserving of phylum status (Van Cleave et al., 1952; Hyman et al., 1951; Rupopert et al., 1994). *Acanthocephala* is placed as a sister group to individual classes within Rotifera based on morphological characters (Lorenzen et al., 1985; Ahlrichs et al., 1995). As the diversity of acanthocephalans is limited to approximately 1,150 described species (Amin, 1985). The basic life cycle is highly conserved among all acanthocephalans and substantial phylogenetic evidence from both morphology and molecular data indicates that acanthocephalans have a close evolutionary relationship with Rotifera (Clement et al., 1985; Lorenzen et al., 1985; Winnepeninckx et al., 1995; Garey et al., 1998; Mark Welch et al., 2000). While acanthocephalans and Rotifers share a syncytial intracytoplasmic lamina, acanthocephalans have none of the other morphological features associated with Rotifers; they lack corona, mastax, digestive tract, toes, and sensory organs, all of which have been used to characterize Rotifer groups. Traditionally acanthocephalans were considered to be related to a number of *pseudocoelomate* animal phyla in the *Aschelminthes* (Hyman et al., 1951; Brusca and Brusca, 1990). Phylogenetic analysis of 18S rRNA sequences demonstrate, however, that the *Aschelminthes* is not monophyletic, and among sampled sequences *Acanthocephala* and Rotifera were recovered as a monophyletic group with substantial branch support (Winnepeninckx et al., 1995). Four morphological features have been presented as apomorphies for a monophyletic Rotifera. *Acanthocephala* clade: (1) syncytial epidermis, (2) intracytoplasmic lamina, (3) sperm cells with flagellum inserted anteriorly, and (4) epidermal cells with apical crypts (Clement et al., 1985; Lorenzen et al., 1985; Nielsen et al., 1996; Wallace et al., 1996; Ahlrichset al., 1997; Garey et al., 1998; Kristensen and Funch, 2000). Phylogenetic investigations of Acanthocephalans have used 18S ribosomal RNA (rRNA) sequence data (Near et al., 1998; Garcia-Varela et al., 2000) and morphological characters (Monks et al., 2001). The molecular phylogenetic analyses result in monophyly for all three sampled Acanthocephalan classes (*Archiacanthocephala*, *Palaeanacanthocephala*, and *Eoacanthocephala*). However, phylogenetic analysis of 138 morphological characters does not result in monophyly of *Archiacanthocephala* (Monks, 2001). Both molecular and morphological analyses support a sister taxon relationship between *Palaeanacanthocephala* and *Eoacanthocephala* (Near et al., 1998; Garcia-Varela et al., 2000; Monks, 2001). Meyer (1932, 1933) grouped the *Acanthocephala* with the Rotifera, *Nematomorpha* and Nematoda under the *Aschelminthes*. Recent molecular studies by (Garey et al. 1996), Garcia Varela et al. (2000), Welch (2000) and Near (2002), among others even suggest that Rotifera and are phylogenetically related sister groups. (Garey et al. 1996) and others, suggested that the *Acanthocephala* represent a taxon within phylum Rotifera. An earlier study using morphological evidence hypothesized that *Acanthocephala* is the sister taxon of the rotifer class Bdelloidea, making Rotifera paraphyletic (Lorenzen et al., 1985). This relationship was also recovered in a preliminary analysis of 18S rRNA sequences sampled from two rotifers, one monogonont and

one bdelloid, and three acanthocephalans (Garey et al., 1996). Bhattacharya (2007) listed 251 acanthocephalan species from India and described a few species and genera, but did not recognize order *Neoechinorhynchida* and included its families under order *Gyracanthocephala*.

CONCLUSION

Acanthocephalans show affinity with Helminthes as well as Rotifers. The general structure is rather on the *Aschelminthic* side, whereas the embryology presents more points of resemblance with the Platyhelminthes. While Acanthocephalans and Rotifers share a syncytial intracytoplasmic lamina, acanthocephalans have none of the other morphological features associated with Rotifers. Recent genome analysis has shown that they are descended from Rotifers and collectively known as *Syndermata*. Phylogenetic evidence from both morphology and molecular data indicates that Acanthocephalans have a close evolutionary relationship with Rotifera. Therefore, *Acanthocephala* can be considered as independent phylum. The most typical forms are *Acanthocephalus*, *Neoechinorhynchus*, *Gigantorhynchus*. Acanthocephalans are regarded as potential model to study the adaptive processes and evolution of parasitism.

References

- Ahlich, W.H. (1995). *Seison annulatus* and *Seison nebaliae*-U1- trastruktur und Phylogenie. *Verh. Deutschen. J. Zool. Ges.*, 88: 115.
- Ahlich, W. H. (1997). Epidermal ultrastructure of *Seison nebaliae* and *Seison annulatus*, and a comparison of epidermal structures within the Gnathifera. *Zoomorphologic*. 117:41–48.
- Amin, O.M. (1982). Acanthocephala. In: *Synopsis and Classification of Living Organisms*. (Ed. S.P. Parker). McGraw-Hill Book Co, New York, pp.933–941.
- Amin, O.M., 1985. In: *Biology of the Acanthocephala* (Ed. D.W.T. Crompton., B.B. Nickol). Cambridge University Press, London and New York, pp: 27–72.
- Amin, O.M., 1985. In: *Biology of the Acanthocephala* (Ed. D.W.T. Crompton., B.B. Nickol). Cambridge University Press, London and New York, pp: 27–72.
- Amin, O.M., Evans P., Heckmann, R.A., El-Naggar A.M. (2013). The description of *Mediorhynchus africanus* n. sp. (Acanthocephala: Gigantorhynchidae) from galliform birds in Africa. *J. Parasitol.* 112:2897–2906.
- Amin, O.M., Heckmann R.A., Ha N.V. (2011). Description of two new species of *Rhadinorhynchus* (Acanthocephala, Radiorhynchidae) from marine fish in Halong Bay, Vietnam, with a key to species. *Acta Parasitol.* 56: 67–77.
- Bhattacharya, S.B. (2007). *Handbook on Indian Acanthocephala*. Kolkata, *Zool. Surv. India*, pp- 255.
- Brusca, G. J, and R. C. Brusca. (1990). *Invertebrates*. Sinauer, Sunderland, Massachusetts.
- Bullock, W.L., 1969. In: *Problems in Systematics of Parasites* (Ed. G.D. Schmidt). University Park Press, Baltimore, pp: 9-43.
- Cholodkovsky, N. A. (1897). Classification of the Acanthocephala. *Trudy San Petersburg. Folia Parasitologica*, pp 28:14–20.
- Clement, P., 1985. In: *The relationships of rotifers*. (Ed. S. C. Morris., J. D. George., R. Gibson., H. M. Platt), Oxford University Press, Oxford, pp: 224–247.
- Dunagan, T. T., D. M. Miller. (1991). In: *Microscopic anatomy of invertebrates* (Ed: F. W. Harrison.), *J Comp. Parasitol.* pp: 21–28.
- García-Varela, M., Cummings M.P., Pérez-Ponce de León G., Gardner S.L., Lacleste J.P. (2002). Phylogenetic analysis based on 18S ribosomal RNA gene sequences supports the existence of class Polyacanthocephala (Acanthocephala). *J. Mol. Evol.* 50: 532–540.
- García-Varela, M., Cummings M.P., Pérez-Ponce de León G., Gardner S.L., Lacleste J.P. (2002). Phylogenetic analysis based on 18S ribosomal RNA gene sequences supports the existence of class Polyacanthocephala (Acanthocephala). *J. Mol. Evol.* 50: 532–540.
- Garey, J. R., T. J. Near, and S. A. Nadler. (1996). Molecular evidence for Acanthocephala as a subtaxon of Rotifera. *J Mol. Evol.*, 43: 287–292.
- Garey, J.R., Schmidt-Rhaesa A., Near T.J., Nadler S.A. (1998). The evolutionary relationships of rotifers and acanthocephalans. *J Hydrobiol.*, 387: 83–91.
- Golvan, Y.J. (1994). Nomenclature of the Acanthocephala. *Res. Rv. in Parasitol.* 54: 135–205.
- Gupta, N.K., Lata V. (1967). Observations on eight already known acanthocephalan parasites from vertebrate hosts. *Res. Bull. Panjab Univ. Sci.* 18:325–341.
- Hyman, L. B., 1951. *The invertebrates, Acanthocephala, Aschelminthes, and Entoprocta*. McGraw-Hill. McGraw-Hill Book Company Inc., New York.
- Khokhlova, I.G. (1986). The acanthocephalan fauna of terrestrial vertebrates of SSSR. *Nauka, Moskva*, pp-276.
- Kristensen, R. M. and P. Funch. (2000). Micrognathozoa: A new class with complicated jaws like those of Rotifera and Gnathostomulida. *J Morph.*, 246:1–49.
- Leuckart, R. (1848). *Über die Morphologie und Verwandtschaftsverhältnisse der wirbellosen Thiere. Ein Beitrag zur Charakteristik und Classification der Thierischen Formen*. F. Vieweg und Sohn, Braunschweig, Germany, pp- 180.
- Lorenzen, S. (1985). In: *The Origins and Relationships of Lower Invertebrates.*, (Ed: SC Morris, JD George, R Gibson, Platt HM). Clarendon Press, New York, pp:210-223.
- Mark Welch, D. B. (2000). Evidence from a protein-coding gene that acanthocephalans are rotifers. *J Invert. Biol.*, 119:17–26.
- Monks, S. (2001). Phylogeny of the Acanthocephala based on morphological characters. *Syst. J. Parasitol.* 48:81–116.

27. Monks S., Pulido-Flores G., Violante-González J. (2011). A new species of *Neoechinorhynchus* (Acanthocephala: Neoechinorhynchidae) in *Dormitator latifrons* (Perciformes: Eleotridae), *Comp. Parasitol.* 78:21-28.
28. Nadler, S.A. (1998). The evolutionary relationships of rotifers and acanthocephalans. *J. Hydrobiologia.* 387:83–91.
29. Near T.J. (2002). Acanthocephalan phylogeny and the evolution of parasitism. *J. Integ. Comp. Biol.* 42: 668–677.
30. Near, T.J., Garey, J.R., Nadler, S.A. (1998). Phylogenetic relationships of the Acanthocephala inferred from 18S ribosomal DNA sequences. *J. Mol. Phylog. Evol.*, 10: 287–298.
31. Nickol, B. B. (1985). Epizootiology. In *Biology of the Acanthocephala* (ED. D. W. T. Crompton and B. B. Nickol), Cambridge University Press, Cambridge, pp. 307–346.
32. Nickol B.B., Crompton D.W.T., Seay D.W. (1999). Reintroduction of *Proflicollis Meyer*, 1931, as a genus in Acanthocephala: significance of the intermediate host. *J. Parasitol.*, 85: 716–718.
33. Nickol B.B., Heard R.W., Smith N.F. (2002). Acanthocephalans from crabs in the southeastern U.S., with the first intermediate hosts known for *Arhythmorhynchus frassoni* and *Hexaglandula corynosoma*. *J. Parasitol.* 88: 79–83.
34. Nielsen, C., Scharff, N., Eiby-Jacobsen, (1996). Cladistic analysis of the animal kingdom. *J. Biol. Linn. Soc.* 57: 385-410.
35. Petrochenko, V. I. (1952). On the position of the Acanthocephala in the zoological system. (Phylogenetic connections of the Acanthocephala with other groups of invertebrates). *Zool. Zh.* 31:288–327.
36. Rudolphi, C.A. (1802). Fortsetzung der Beobachtungen über die Eingeweidwürmer. *J. Arch. Zool. Zootom.* 2: 1–67.
37. Ruppert, E.E., Barnes, R.D., 1994. *Invertebrate Zoology*. Harcourt Brace, Orlando. Pp: 1056.
38. Schmidt, G.D., Dailey M.D. (1971). A zoogeographic note on the acanthocephalan *Corynosoma bullosum* (von Linstow, 1892). *J. Trans. Amer. Microsc. Soc.* 90: 94–95.
39. Schmidt, G. D., 1985. In: *Development and life cycles*. (Ed D. W. T. Crompton, B. B. Nickol.), Cambridge University Press, Cambridge. pp: 273–286.
40. Skrjabin K.I., Shults R.E.S. (1931). *Helminthoses of Man (Foundations of Medical Helminthology) for Medical Doctors and Veterinarians, Biologists and Students. Part II.* State Medical Publisher, Moscow and Leningrad, pp-250.
41. Starling, J. A., and F. M. Fisher, Jr. (1975). Carbohydrate transport in *Moniliformis dubius* (Acanthocephala). I. The kinetics and specificity of hexose absorption. *J. Parasitol.* 61: 977–990.
42. Thapar, G.S. (1927). On *Acanthogyrus* n. gen. from the intestine of the Indian fish *Labeo rohita*, with a note on the classification of the Acanthocephala. *J. Helminthol.* 5: 109–120.
43. Van Cleave, H.J., Rausch R L. (1951). The Acanthocephala of eider ducks. *J. Proc. Helminthol. Soc. Wash.*, 18: 81–84.
44. Van Cleave, H.J. (1952). Acanthocephalan nomenclature introduced by Lauro Travassos. *J. Proc. Helminthol. Soc. Wash.*, 19:1–8.
45. Van Cleave, H.J. (1953). Acanthocephala of North American mammals. III. *J. Biol. Monogr.* 23: 1–179.
46. Verweye, N. L., Klimpe, I. S., Palm, H.W. (2011). Molecular phylogeny of the Acanthocephala (class Palaeacanthocephala) with a paraphyletic assemblage of the orders Polymorphida and Echinorhynchida. *PLoS ONE* 6: e28285.
47. Wallace, R. L., Ricci, C. G. Melone. (1996). A cladistic analysis of pseudocoelomate (aschelminth) morphology. *J. Invert. Biol.* 115:104–112.
48. Wang, P.Q. (1986). Notes on Acanthocephala from Fujian, with descriptions of three new species. *J. Wuyi Sc.* 6: 181–192.
49. Welch, D.B.M. (2000). Evidence from a protein-coding gene that acanthocephalans are rotifers. *J. Invert. Biol.* 119: 17–26.
50. Winnepeninckx, B. T., Backeljau, L. Y., Mackey, J. M., Brooks, R.D., Wachter, S. Kumar., J. R. Garey. (1995). 18S rRNA data indicate that Aschelminthes are polyphyletic in origin and consist of at least three distinct clades. *Mol. Biol. Evol.*, 12:1132–1137.