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The morphological and molecular description of *Neoechinorhynchus* (*Neoechinorhynchus*) *poonchensis* sp. n. from *Schizothorax richardsonii* (Gray) in Poonch, Jammu and Kashmir, India

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Abstract: Specimens of *Neoechinorhynchus* (*Neoechinorhynchus*) *poonchensis* sp. n. are described from *Schizothorax richardsonii* (Gray) in the Poonch River, Jammu and Kashmir. Specimens are thick-walled with dissimilar dorsal and ventral para-receptacle structures, anteriorly manubriated hooks, two giant nuclei in each lemniscus and many subcutaneousy. The lemnisci barely overlap the larger anterior testis, the cement gland has eight giant nuclei, and the seminal vesicle is large with thin walls. The vagina is unremarkable but the long uterus is made up of four specialised regions. *Neoechinorhynchus rigidus* (Van Cleave, 1928), resembles *N. poonchensis* sp. n. It is distinguished from *N. poonchensis* sp. n. by having smaller trunk, proboscis, and male reproductive structures, equal testes, unequal lemnisci with three giant nuclei each, and much larger anterior proboscis hook (130 µm in males) than that originally described by Van Cleave (1928) (70 µm in a female). Anterior hook length alone is sufficient to conclude that the *N. rigidus* of Datta (1937) is not the same species as the *N. rigidus* of Van Cleave (1928). Van Cleave's (1928) species remains valid and that of Datta (1937) is considered a different species named *Neoechinorhynchus pseudorigidus* sp. n., herein. Micropores of *N. poonchensis* sp. n. have variable distribution in different trunk regions and the Energy Dispersive X-ray analysis demonstrated higher levels of sulfur and lower levels of calcium and phosphorus. Sequences of the 18S rDNA gene from nuclear DNA, and cytochrome c oxidase subunit I (*cox1*) from mitochondrial DNA of *N. poonchensis* sp. n. were amplified and aligned with other sequences available on GenBank. Maximum likelihood (ML) and Bayesian inference (BI) analyses inferred for 18S rDNA and *cox1* showed that *N. poonchensis* sp. n. was nested in a separate clade.

Keywords: Taxonomy, morphology, SEM, 18S rDNA, *cox1*, EDXA, fish, Indomalayan region

A few species of *Neoechinorhynchus* Stiles et Hassall, 1905 have been described since the revision of Amin (2002) recognised two subgenera, *Neoechinorhynchus* and *Hebesoma* Van Cleave, 1928, included keys to 88 species, transferred six species to other genera, and declared 14 species as invalid. Naidu (2012) listed 93 species of *Neoechinorhynchus* (*Neoechinorhynchus*) based on Amin (2002) and included 32 species occurring in the Indian subcontinent. Some of these, however, have been relegated to other genera such as *Acanthogyrus* (*Acanthosentis*) *kashmirensis* Amin, Heckmann et Zargar, 2017 (= *Neoechinorhynchus kashmirensis* Fotedar et Dhar, 1977). The present paper adds one more species to the Indian fauna of the subgenus *Neoechinorhynchus* and also delegates a misidentified species to another. We provide the morphological and molecular description of a new species of *Neoechinorhynchus* collected from the snow trout in the Jammu and Kashmir area at the present border line between India and Pakistan. The new acanthocephalan species bears some superficial morphological similarities to *Neoechinorhynchus rigidus* (Van Cleave, 1928) described by Van Cleave (1928) from one female specimen from a close host species in a related area in India. Datta (1937) later on redescribed what he believed to be the same species from male specimens without providing any figures or line drawings. Datta's description, routinely quoted by subsequent observers who regularly copy Van Cleave's (1928) figures, had become the standard description of this species. Datta's account

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creates a lot of confusion not previously detected/reported by other observers. We seek to clear up this confusion and restore the proper taxonomic status of Datta's "*N. rigidus*" to its proper position. We also provide a complete description of our new species with SEM images, line drawings with emphasis on newly observed features including, but not limited to, the micropores, Energy Dispersive X-ray analysis (EDXA) of hooks, para-receptacle structures, and molecular analysis. The EDXA data provides a diagnostic chemical baseline that proved to have a significant diagnostic value (Amin et al. 2019c). In the present study, morphological and molecular characterisation of *Neoechinorhynchus* (*Neoechinorhynchus*) *poonchensis* sp. n. collected from *Schizothorax richardsonii* (Gray) was performed. The study also inferred the phylogenetic position using 18S rRNA and *cox1* gene markers within the genus *Neoechinorhynchus*.

MATERIALS AND METHODS

Specimen collection

A total of nine acanthocephalans were collected from five of 16 examined snow trout, *Schizothorax richardsonii* (Gray) (Cyprinidae), in the Poonch River, Jammu and Kashmir, India at the border line near LOC (33.2778N, 75.3412E) in January, 2021. The specimens were collected from freshly caught fish intestine using a dissecting scope. Six specimens (two males and four females) were processed for microscopy after having been kept in water overnight or until fully extended, and then fixed in cold 70% ethanol. Worms were punctured with a fine needle and subsequently stained in Mayer's acid carmine, destained in 4% hydrochloric acid in 70% ethanol, dehydrated in ascending concentrations of ethanol (24 hr each), and cleared in 100% xylene and then in 50% Canada balsam and 50% xylene (24 hr each). Whole worms were then mounted in Canada balsam. Measurements are in micrometres, unless otherwise noted; the range is followed by the mean values between parentheses. Width measurements represent maximum width. Trunk length does not include proboscis, neck, or bursa. One female specimen was processed for SEM and EDXA, and two for molecular analysis as outlined below.

Optical microscope images

Optical microscope images were acquired using a BH2 light Olympus microscope (Olympus Optical Co., Okaya, Nagano, Japan) attached to an AmScope 1,000 video camera (United Scope LLC, dba AmScope, Irvine, California), linked to an ASUS laptop equipped with HDMI high-definition multimedia interface system (Taiwan-USA, Fremont, California). Images from the microscope were transferred from the laptop to a USB and stored for subsequent processing on a computer.

Line drawings

Line drawings were made by using a Ken-A-Vision micro-projector (Ward's Biological Supply Co., Rochester, New York) which uses cool quartz iodine 150W illumination with 10×, 20×, and 43× objective lenses. Images of stained whole mounted specimens were projected vertically on 300 series Bristol draft paper (Starthmore, Westfield, Massachusetts), then traced and inked with India ink. Projected images were identical to the actual specimens being projected.

Scanning electron microscopy (SEM)

One female that had been fixed and stored in 70% ethanol was processed for SEM following standard methods (Lee 1992). That specimen turned out to be somewhat fragile with the proboscis mostly retracted in the praesoma. This proboscis was extracted using Gallium beam to expose it and allow further work on the hooks to take place. These included critical point drying (CPD) (Tousimis Automandri 931.GL) and mounting on aluminum SEM sample mount (stub) using conductive double-sided carbon tape. The sample was sputter-coated with an 80%–20% gold-palladium target for three minutes using a sputter coater (Quorum (Q150T ES) www.quorumtech.com) equipped with a planetary stage, depositing an approximate thickness of 20 nm. Sample was placed and observed in an FEI Helios Dual Beam Nanolab 600 Scanning Electron Microscope (FEI, Hillsboro, Oregon). The sample was imaged using an accelerating voltage of 5 kV, and a probe current of 86 pA, at high vacuum using a SE detector.

Focused Ion Beam (FIB) sectioning of hooks

A dual-beam SEM with gallium (Ga) ion source (GIS) is used for the Liquid Ion Metal Source (LIMS) part of the process. The gallium beam (LIMS) is a gas injection magnetron sputtering technique whereby the rate of cutting can be regulated. The hooks were sectioned at two positions (Tip and Middle) using the FEI Helios Dual Beam Nano lab mentioned above. The dual-beam FIB/SEM is equipped with a gallium (Ga) LIMS. The hooks of the acanthocephalans were centred on the SEM stage and cross-sectioned using an ion accelerating voltage of 30 kV and a probe current of 2.7 nA. The time of cutting was based on the nature and sensitivity of the tissue. The sample also went through a cleaning cross-section milling process to obtain a smoother surface. The cut was analysed with an X-ray normally at the tip, middle and base of hooks for chemical ions with an electron beam (Tungsten) to obtain an X-ray spectrum. The intensity of the GIS was variable according to the nature of the material being cut. Results were stored with the attached imaging software.

Energy Dispersive X-ray Analysis (EDXA)

The Helios Nano lab 600 is equipped with an EDAX (Mahwah, NJ) TEAM Pegasus system with an Octane Plus detector. The sectioned cuts were analysed by EDXA. Spectra of selected areas were collected from the centre and the edge of each cross-section. EDXA spectra were collected using an accelerating voltage of 15 kV, and a probe current of 1.4 nA. Data collected included images of the displayed spectra as well as the raw collected data. Relative elemental percentages were generated by the TEAM software.

Type specimens

Type specimens were deposited in the University of Nebraska's State Museum's Harold W. Manter Laboratory (HWML) collection, Lincoln, Nebraska.

Molecular methods

DNA was extracted from two specimens using QIAGEN DNeasy™ tissue kit (Qiagen, Hilden, Germany) according to man-

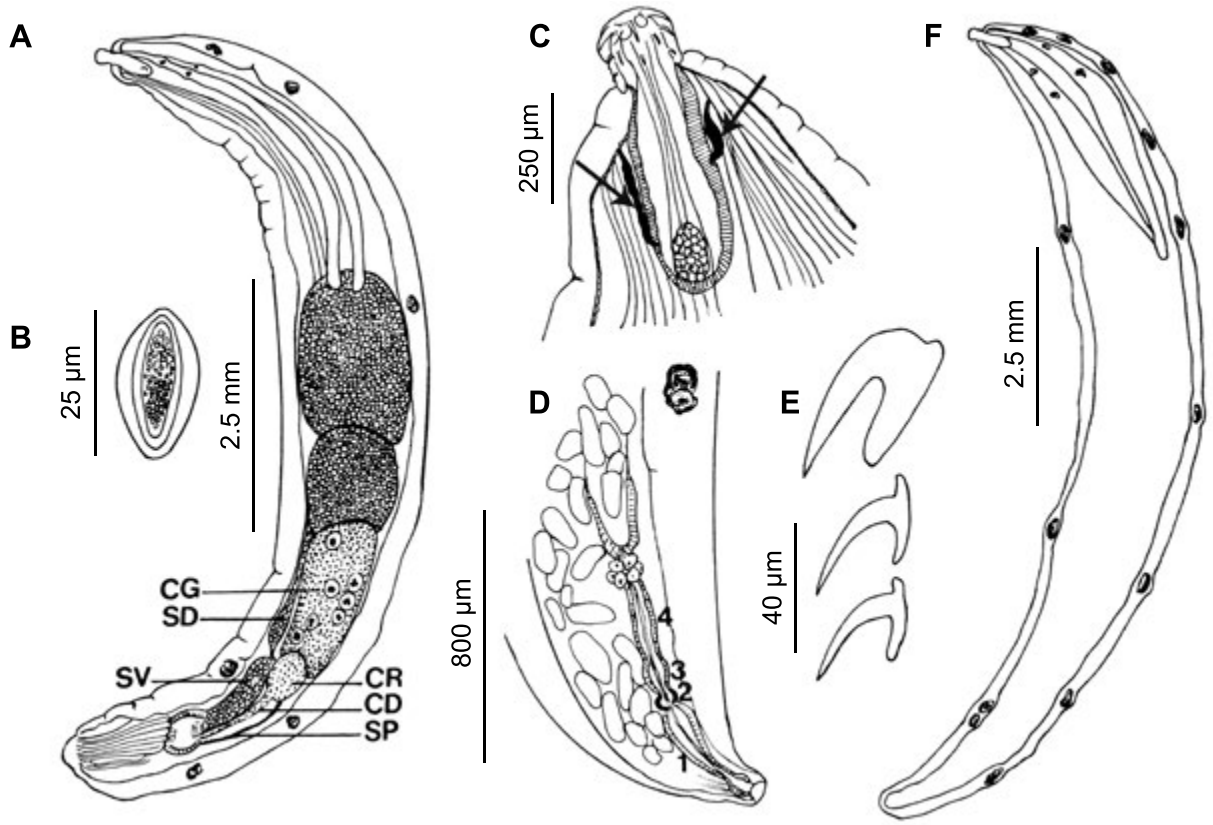

Fig. 1. Line drawings of specimens of *Neoechinorhynchus poonchensis* n. sp. from *Schizothorax richardsonii* (Gray) in Jammu-Kashmir. **A** – holotype male. Note the relative size of testes, the posterior extent of the equal lemnisci to the anterior edge of anterior testis, and the labeled parts of the reproductive system. CD – cement duct, CG – cement gland with 8 nuclei, CR – cement reservoir, SD – sperm duct, SP – Saefftigen's pouch, SV – seminal vesicle; **B** – ripe egg; **C** – the anterior portion of a female specimen showing the short dorsal para-receptacle structure (PRS), long ventral PRS (arrows) and many longitudinal muscle fibres masking the insertion of the dorsal PRS into the body wall anteriorly; specimen with the fewest giant hypodermal nuclei (4 dorsal and 1 ventral); **D** – reproductive system of a female in the ovarian ball stage; the four parts of the uterus are numbered; **E** – one longitudinal row of manubriated hooks; **F** – allotype female showing the largest number of giant hypodermal nuclei noted in this acanthocephalan species (9 dorsal and 4 ventral).

ufacturer's instructions. 18S rDNA region of nuclear ribosomal DNA (rDNA) was amplified using the primers 18SU467F (forward, 5'-ATCCAAGGAAGGCAGCAGGC-3'); 18SL1310R (reverse, 5'-CTCCACCAACTAAGAACGGC-3') (Suzuki et al. 2008) and WormA (forward, 5'-GCGAATGGCTCATTAAATCAG-3'); 1,270R (forward, 5'-CCGTCAATTCCTTTAAGT-3') (Littlewood and Olson 2001). The thermocycling conditions were as follows: an initial denaturation at 94 °C for 3 min followed by 35 cycles for 40 s at 94 °C, for 1 min at 56 °C for both primers mentioned above for annealing, and extension for 7 min at 72 °C, and then stored at 4 °C.

Mitochondrial *cox1* gene was amplified using the primers LCO1490 (forward, 5'-GGTCAACAAATCATAAAGATATTGG-3') and HCO2198 (reverse, 5'-TAAACTTCAGGGTGACCAAAAAATCA-3') (Folmer et al. 1994) using the above PCR profile except 45 °C was used for primer annealing. PCR reactions were performed containing a volume of 25 µl that comprises 1 µl of each primer, 2.5 µl of 10 X buffer including $MgCl_2$, 3 µl of dNTPs (10 mM), 0.9 µl of 1 U of Taq DNA polymerase (Biotools, Spain) with 3 µl of the genomic DNA and 13.6 µl of distilled water. The sequencing reactions were performed with the same primers mentioned above using an ABI Big Dye Terminator Kit (Applied Biosystems, Foster City, California) according to manufacturer's protocol.

Newly generated contiguous sequences were assembled and edited using Geneious R10 (https://www.geneious.com). Sequences of 18S rDNA and *cox1* gene were deposited in GenBank under the accession numbers MZ322841, MZ322842, MZ323422, MZ323421. Sequences obtained for 18S rDNA and *cox1* were aligned using ClustalW with default parameters implemented in MEGA v7 (Kumar et al. 2016) with sequences from other closely related species. The detail about the sequences used in the alignment and phylogenetic analysis is mentioned in Table 3. *Polyacanthorhynchus caballeroi* Diaz-Ungria et Rodrigo, 1960 (DQ089724 and AF388660) and *P. nigerianus* Echi, Suresh, Sanil, Iyaji, Nwani et Ejere, 2015 (KC904074) were selected as outgroup.

GUIDANCE (Penn et al. 2010), a web based program, was used to evaluate alignment reliability and the aligned sequences were used for further phylogenetic analysis. Phylogenetic trees were constructed through maximum likelihood (ML) and Bayesian inference (BI) analyses based on GTR + I + G model for 18S rDNA and *cox1* nucleotide datasets. The jModelTest 2.1.4 (Darriba et al. 2012) that is based on Akaike information criterion (AIC) was used to estimate the best-fitting model of nucleotide

Table 1. Morphometric and descriptive comparisons between specimens of *Neoechinorhynchus poonchensis* sp. n. and *Neoechinorhynchus pseudorigidus* sp. n. in India.

Species	***Neoechinorhynchus poonchensis* sp. n.**	***Neoechinorhynchus pseudorigidus* sp. n.**
Host	*Schizothorax richardsonii* (Gray)	*Schizothorax zarudnyi* (Nikolskii)
Source	This paper	Datta (1937) n. comb.
Other references		Datta (1936), Van Cleave (1928), Naidu (2012)
Sample size	2 males, 4 females	12 males
Location	Poonch River, Jammu and Kashmir, India	Seistan and Hamun-i-Helm and near Labi
Males		
Trunk L × W (mm)	7.12–9.25 (8.18) × 1.10–1.25 (1.17)	2.4–7.5 × 0.65–0.95
Body wall thickness	175–225 (200)	
Cuticular nuclei	5–9 (7) dorsal, 1–4 (2) ventral	8–9 dorsal, 1–2 ventral
Proboscis L × W	112–120 (116) × 112–127 (120)	121 × 110 (Datta: 1.21 × 1.10 mm)
Hook L (ant., mid., post.)	57–60 (58), 37–39 (38), 40 (40)	130, 50, 45 Anterior hook much longer
Hook root L (anterior, middle, posterior)	40–42 (41), 27–28 (27), 29–30 (29)	
Proboscis receptacle L × W	406–458 (432) × 166–177 (171)	350 × 220
Para-receptacle structure	Dorsal and ventral; dissimilar	
Lemnisci L × W (mm)	Equal: 2.65–3.07 (2.86) × 0.16–0.32 (0.24)	Unequal: 4.31 × 0.24 and 3.92 × 0.24
Lemnisci description	Reach ant. testis; not attached to body wall	Reach posterior testis
Giant lemniscal nuclei	2 in each	3 in each
Anterior testis L × W (mm)	1.50–1.52 (1.51) × 0.75–0.87 (0.81)	1.12 × 0.65 Testes equal, more slender
Posterior testis L × W (mm)	0.97–1.00 (0.98) × 0.72–0.73 (0.72)	1.10 × 0.70
Cement gland L × W (mm)	0.83–1.55 (1.19) × 0.55–0.62 (0.59)	0.79 × 0.40
Cement gland nuclei	8	6–8
Cement reservoir	333–364 (348) × 208–364 (286)	240 × 150
Seminal vesicle L × W	624–780 (702) × 177–364 (270)	620 × 220
Saefftigen's pouch L × W	860–936 (898) × 156–164 (160)	
Females		
Trunk L × W (mm)	11.37–15.00 (13.37) × 1.37–2.37 (1.86)	9.00 ×0.87 (Van Cleave 1928)
Body wall thickness	175–225 (200)	
Cuticular nuclei	5–9 (7) dorsal, 1–4 (2) ventral	8–9 dorsal, 1–2 ventral
Proboscis L × W	130–147 (141) × 142–147 (144)	
Hook L (ant., mid., post.)	62–72 (67), 38–45 (42), 38–45 (40)	
Hook root L (ant., mid., post.)	45–50 (48), 23–28 (26), 25–33 (30)	
Shape of hook roots	Elongate with anterior manubria	Ovoid; no manubria (Van Cleave 1928, Fig.2)
Proboscis receptacle L × W	468–478 (473) × 187–229 (208)	
Para-receptacle structure	Dorsal and ventral; dissimilar	
Lemnisci L × W (mm)	3.17–3.75 (3.48) × 0.26–0.37 (0.33)	
Giant lemniscal nuclei	2 in each	3 in each
Reproductive syst.	11.4% of trunk length	"similar to *N. devdevi"* (Datta 1936; below)
Vagina L	104, short, weak	500, thick-walled, muscular
Uterus L	832, long, in 4 specialized parts	250, "flabby", short
Uterine bell L	364, inversed bell-shaped, not attached to body wall	415, funnel-shaped with large guard cells
Gonopore L × W	Terminal	"postero-ventral; as in *N. devdevi*"
Eggs L × W	22–27 (24) × 13–15 (14)	27–30 × 12–15 (Naidu 2012)

* Range (mean) in micrometres unless otherwise stated.

substitution. Maximum likelihood analyses were performed using MEGA v.7 with bootstrap validation on 1,000 replications. Bayesian inference analyses were performed using Topali v2.5 (Milne et al. 2009). Log likelihoods were estimated using Markov chain Monte Carlo (MCMC) search on two simultaneous runs of four chains over 1,000,000 generations with every 100th tree saved. The burn in was set to 25. The pairwise genetic distances (p-distance) were calculated using the 'uncorrected P-distance' model implemented in MEGA v7.

RESULTS

Morphological description of *Neoechinorhynchus* (*Neoechinorhynchus*) *poonchensis* sp. n. Figs. 1–3

ZooBank number for species:
urn:lsid:zoobank.org:act:32907587-8639-4AF1-9746-D73D467FD107

General. Neoechinorhynchidae. With characters of the genus *Neoechinorhynchus* and the subgenus *Neoechinorhynchus* as described by Amin (2002). With prominent sexual dimorphism in size of shared structures. Trunk cylindrical and slender, slightly but definitely wider at middle, tapering towards both ends (Fig. 1A,F), with many longitudinal muscles (Fig. 1C). Body wall thick (Fig. 1A,C,D,F), with osmiophilic micropores throughout, variable in different parts of the trunk (Fig. 3A–C). Giant hypodermal nuclei many dorsally and fewer ventrally (Fig. 1A,F).

Proboscis about as long as wide (Figs. 1C, 2A). Anterior hooks long at latero-apical end of proboscis compressed laterally near base (Fig. 2D) with tip bent ventrally (Fig. 2C). Root of anterior hook simple, shorter than blade, posteriorly directed with knob-shaped anterior manubrium (Fig. 1E). Middle and posterior hooks smaller and more slender, almost equal, with elongate posteriorly directed roots having prominent anterior manubria (Fig. 1E). Hooks with thin cortical layer and solid but partially vacuolated core (Fig. 2D).

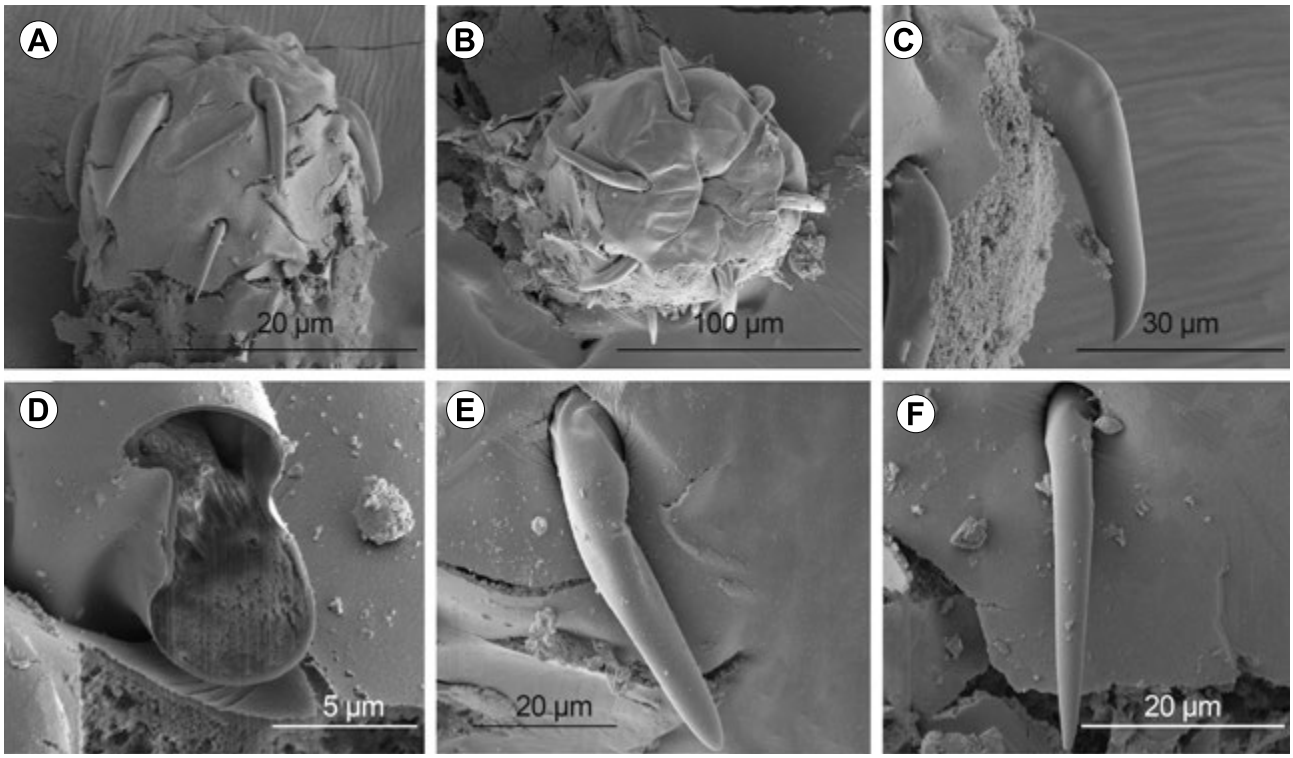

Fig. 2. SEM of a female specimen of *Neoechinorhynchus poonchensis* sp. n. from *Schizothorax richardsonii* (Gray) in Jammu-Kashmir. **A** – a lateral view of a partially damaged proboscis extracted from the praesoma; **B** – an apical view of the same proboscis suggesting the possible presence of an apical organ; **C** – the anterior hook; note the curved tip and the dorsal lateral constriction; **D** – a gallium cut section near the base of an anterior hook showing its thin cortical layer, dense bottom core and the lateral constriction; **E** – a view of the middle hook; **F** – posterior hook.

Neck unremarkable. Proboscis receptacle about three times as long as proboscis, with dorsal wall markedly thicker than ventral wall, ovoid cephalic ganglion at its base, and two dissimilar para-receptacle structures (PRS) on both sides. Ventral PRS long with insertion near posterior end of receptacle; dorsal PRS short inserting near middle of receptacle (Fig. 1C). Lemnisci long, about same length, wider near middle, with two prominent ovoid giant nuclei each and no fibrillar attachment to body wall (Fig. 1A,F). Gonopore terminal in males and females (Fig. 1A,D).

Males (based on two adult specimens; see Table 1 for measurements). Body wall 175–225 (200) thick with 5–9 dorsal and 1–4 ventral giant hypodermal nuclei. Lemnisci equal extending to anterior end of anterior testis (Fig. 1A). Reproductive system in posterior two thirds of trunk with two large contiguous testes filling width of body cavity. Anterior testis markedly larger than posterior testis. Contiguous cement gland rectangular; with eight large spherical nuclei. Cement reservoir prominent, round, at posterior end of cement gland followed posteriorly by marked cement gland duct draining into bursa along with large ventral sac-shaped sperm vesicle, overlapping dorsally Saefftigen's pouch (Fig. 1A). Bursa retracted.

Females (based on four adults; three gravid with eggs and one with ovarian balls; see Table 1 for measurements and counts). Body wall 250–375 (306) thick with 7–10 dorsal and 2–4 ventral giant hypodermal nuclei. Reproductive system 1.3 mm long, 11.4% of trunk length of one female with ovarian balls, with weak vaginal sphincter, uterus with four specialised regions, few large uterine bell glands of selector apparatus, and moderate bell-shaped uterine bell not attached to body wall ventrally or dorsally (Fig. 1D). Uterine regions partially evident in gravid specimens. Eggs ovoid with blunt poles and no prolongation of fertilisation membrane (Figs. 1B, 3D).

Type host: Common snow trout *Schizothorax richardsonii* (Gray) (Cyprinidae: Barbinae).

Site of infection: Throughout the intestine.

Type locality: Poonch River, Jammu and Kashmir, India by the border line near LOC (33.5°N 75.0°E).

Specimens deposited: Holotype male, allotype female (in ovarian balls stage) and a gravid paratype female on one slide in the HWML (Collection no. 216543).

Etymology: The new species is named for the Poonch River where it was captured from the type host.

DNA sequences: The newly generated sequence were deposited in GenBank under the following accession numbers: 18S rDNA MZ322841 (1140 bp), MZ322842 (1,130 bp); *cox1* MZ323422 (558 bp), MZ323421 (564 bp).

Taxonomic comparisons

Our new acanthocephalan species, *Neoechinorhynchus poonchensis* sp. n., collected from *Schizothorax richardsonii* in Jammu and Kashmir stream bears some superficial morphological similarities to *Neoechinorhynchus rigidus* described by Van Cleave (1928) from one female specimen from *Schizothorax zarudnyi* (Nikolskii) in Seistan. Van

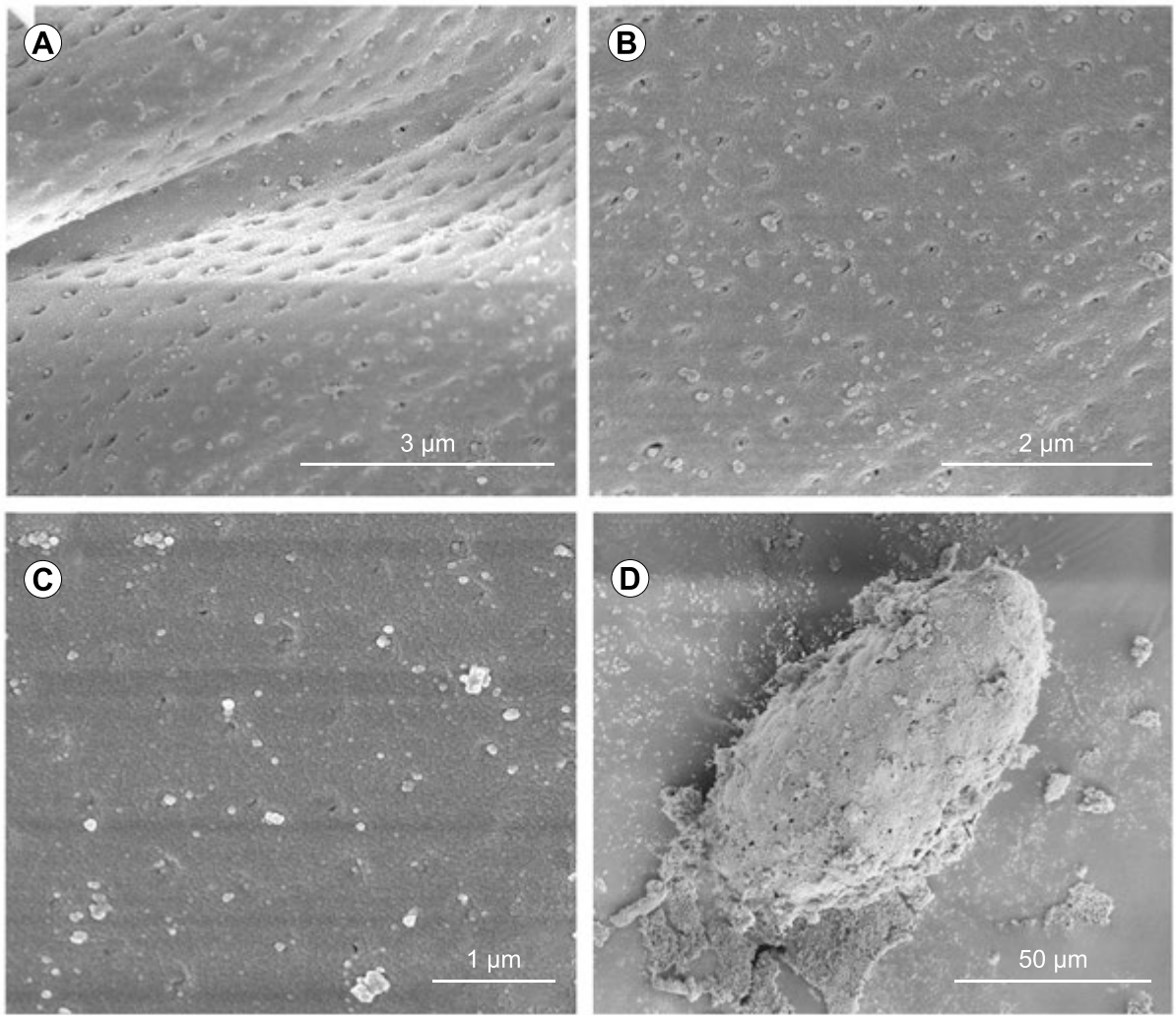

Fig. 3. SEM of a female specimen of *Neoechinorhynchus poonchensis* sp. n. from *Schizothorax richardsonii* (Gray) in Jammu-Kashmir. **A**–**C** – variable patterns of micropore size and distribution in various trunk regions: anterior, middle and posterior trunk, respectively; note the almost linear pattern in A; **D** – an egg covered with debris with the same size and shape observed in microscopic specimens and Fig. 1B.

Cleave's (1928) specimen was a young female in the ovarian ball stage (his fig. 1) with the following dimensions: trunk 9.0 × 0.87 mm, proboscis 192 × 153 µm, and hook length from anterior 70, 47, 41 µm with ovoid roots without manubria (his fig. 2). His female was considerably different from those of *N. poonchensis* in being considerably more slender, proboscis markedly longer than wide, and the ovoid hook roots lacked manubria. Because of the potential inadequacies in comparing our specimens with Van Cleave's (1928) single female, we provided a comparison with Datta's (1937) redescription of *N. rigidus* (Table 1).

Datta (1937) redescribed what he believed to be *N. rigidus* from the same host species and the same geographical location in Seistan as Van Cleave's (1928) *N. rigidus*, from 12 male specimens without providing any figures or line drawings. Datta (1937) also collected 23 female specimens that he made no reference to in his redescription except to mention that "the female genitalia agrees with the description of *Eosentis devdevi* Datta, 1936 of the author (1936)". Datta's description, routinely quoted by subsequent observers who regularly copied Van Cleave's (1928) two figures, has become the standard description of this species. Datta's account creates a lot of confusion not previously detected/reported by other observers for the following reasons. Datta (1937) stated that "The identification (of *N. rigidus*) was confirmed by examination of the holotype (Van Cleave's single female) in the collections of the Indian Museum". We do not see how the description of Datta's 12 males be confirmed by the examination of a single female from another collection by Van Cleave. The anterior proboscis hook in Datta's males measured 130 while that of Van Cleave's female was 70. Normally, females have longer hooks than males. Datta (1937) made no reference to hook roots. This and other discrepancies between Datta's (1937) measurements of males and the few measurements available in Van Cleave (1928) account demonstrates that Datta's *N. rigidus* is not Van Cleave's *N. rigidus*. We conclude that Van Cleave's *N. rigidus* has priority and it remains valid despite its meagre description, and that Datta's (1937) *N. rigidus* is another species to be appropriately named, herein, *Neoechinorhynchis pseudorigidus* sp. n. Morphometric comparisons between *N. poochensis*

sp. n. and *N. pseudorigidus* (Table 1) demonstrate the distinguishing differences between these two species notably: the comparative differences between the size of anterior vs. posterior testis, equal vs. unequal lemnisci, lemnisci with 2 *vs*. with 3 giant nuclei, size of anterior hooks, size of cement gland and of cement reservoir, terminal vs. subterminal position of female gonopore, and specialisation of uterus parts. Specimens of *N. poochensis* sp. n. are also characterised by very thick body wall, by having two dissimilar PRS, and elongate hook roots with anterior manubria that may have been difficult to observe or easy to dismiss by Datta's (1937).

There are two other species of *Neoechinorhynchus* that have been described from *Schizothorax* spp. in the Kashmir Valley, India that could be confused with *N. poonchensis*: *Neoechinorhynchus devdevi* (Datta, 1936) and *Neoechinorhynchus yalei* (Datta, 1936). According to Amin (2002), *N. yalei* is considered a synonym of *N. devdevi*. The main anatomy tallies with the description of *E. devdevi*, except in measurements and in the number of subcuticular nuclei. Both species were collected from the same genus of host (Datta 1936) in the same locality and variations in measurements and giant nuclei number fall within the usual intraspecific range". Compared to morphometrics of *N. poonchensis* (Table 1), *N. devdevi* is distinguished by having a considerably smaller trunk (males 2.29–3.30 mm long, females 2.97–7.59 mm) and smaller receptacle (264 × 132 μm), smaller and equal testes (616–704 × 440 μm) (his fig. 6a), smaller and unequal lemnisci (1.78 and 1.87 mm), and longer anterior hooks (90, 45, 40 μm from anterior), smallerer eggs (20 × 5 μm), no demonstrable PRS (his fig. 6b), and female gonopore at the "postero-ventral end."

Remarks. A distinguishing feature females of the new species is the presence of a highly specialised uterus featuring four diverse segments (Fig. 1D). The numerous longitudinal muscle strands in the body cavity of males and females have not been commonly observed in other species of *Neoechinorhynchus*. More unusual are the well-developed roots of all hooks with prominent manubria, especially in the smaller hooks in the middle and posterior circles as has also been found in *Neoechinorhynchus* (*Hebesoma*) *personatus* Tkach, Sarabeev et Shvetsova, 2014 from Tunisia (Amin et al. 2020b, fig. 9) and *Neoechinorhynchus ponticus* Amin, Sharifdini, Heckmann, Rubtsova et Chine, 2020 from the Black Sea (Amin et al. 2020b, fig. 10). In most other members of this genus that we have studied, posterior hooks have vestigial or no roots and anterior hooks are without manubria. Examples include *Neoechinorhynchus cylindratus* (Van Cleave, 1913) from Peru (Amin et al. 2021c), *Neoechinorhynchus didelphis* Amin, 2001 from Georgia, USA (Amin 2001), *Neoechinorhynchus iraqensis* Amin, Al-Sady, Mhaisen et Bassat, 2001 from Iraq (Amin et al. 2001), *Neoechinorhynchus idahoensis* Amin et Heckmann, 1992 from Idaho, USA (Amin and Heckmann 1992), *Neoechinorhynchus robertbaueri* Amin, 1985 from Wisconsin, USA (Amin 1985) and *Neoechinorhynchus ampullatus* from Vietnam (Amin et al. 2011a).

Micropores

The trunk of *N. poonchensis* has apparent osmiophilic micropores of various diameters, shapes and distribution in various parts. In some areas, the micropores are more widely spaced compared to the usual more widely distributed micropores more often observed in other acanthocephalan species.

Para-receptacle structures (PRS)

The PRS are here reported in another species of *Neoechinorhynchus* from India. Like other species of *Neoechinorhynchus*, *Acanthosentis* Verma et Datta, 1929, *Pallisentis* Van Cleave, 1928, *Tenuisentis* Van Cleave, 1936, and *Intraproboscis* Amin, Heckmann, Sist et Basso, 2021, *N. poonchensis* also has a weak single-wall proboscis receptacle in which PRS are found. The uncommon organisation of the PRS in *N. poonchensis* features a ventral long one inserting at the posterior end of the receptacle, and a shorter dorsal one inserting about the middle of the receptacle (Fig. 1C).

Energy Dispersive x-ray analysis (EDXA)

The EDXA results of the hook sections (Table 2) of *N. poonchensis* show a centre core with relatively high level of sulfur surrounded by higher sulfur levels at the exterior. The EDXA spectra of the tip of the hook showed a significantly higher relative concentration of sulfur compared to the centre core of the hook cross-section. The EDXA spectra of the edge of the mid-hook cross-section again show the high-sulfur relative concentration observed in the tip of the hook as well as the marked concentrations of calcium and phosphorus characteristic of the centre core of the mid-hook cross-section. The presence of sulfur, calcium, and phosphorus in the EDXA spectra obtained from the edge of the hook base cross-section is attributed to the proximity of the exterior shell to the centre core. The relative WT% concentrations obtained by the TEAM software are reported in Table 2. It is worth noting that these reported WT% numbers should not be interpreted as compositional. They are, however, indicative of general compositional differences observed between the selected areas.

Molecular results

Two partial 18S rDNA sequences were generated from two isolates of *N. poonchensis*. There are no intraspecific divergences among the newly generated sequences from isolates of *N. poonchensis*. Both methods, ML and BI, present congruent topologies. Therefore, only the ML tree is presented in Fig. 4. The phylogenetic tree from the 18S rDNA dataset shows that *N. poonchensis* isolates form a separate clade from other species with high nodal support values of ML and BI (Fig. 4). Newly obtained sequences of *N. poonchensis* were found to be closer to these *Neoechinorhynchus yamagutii* Tkach, Sarabeev et Shvetsova, 2014 (MN149220) from *Mugil cephalus* Linnaeus in Russia and shows 0.68% divergence. The isolates of *N. poonchensis* are also sister to other congeneric species with genetic divergence observed as 1.0– 1.8% with species of *Neoechinorhynchus* (MN992023–MN992025) from India, and 2.1%

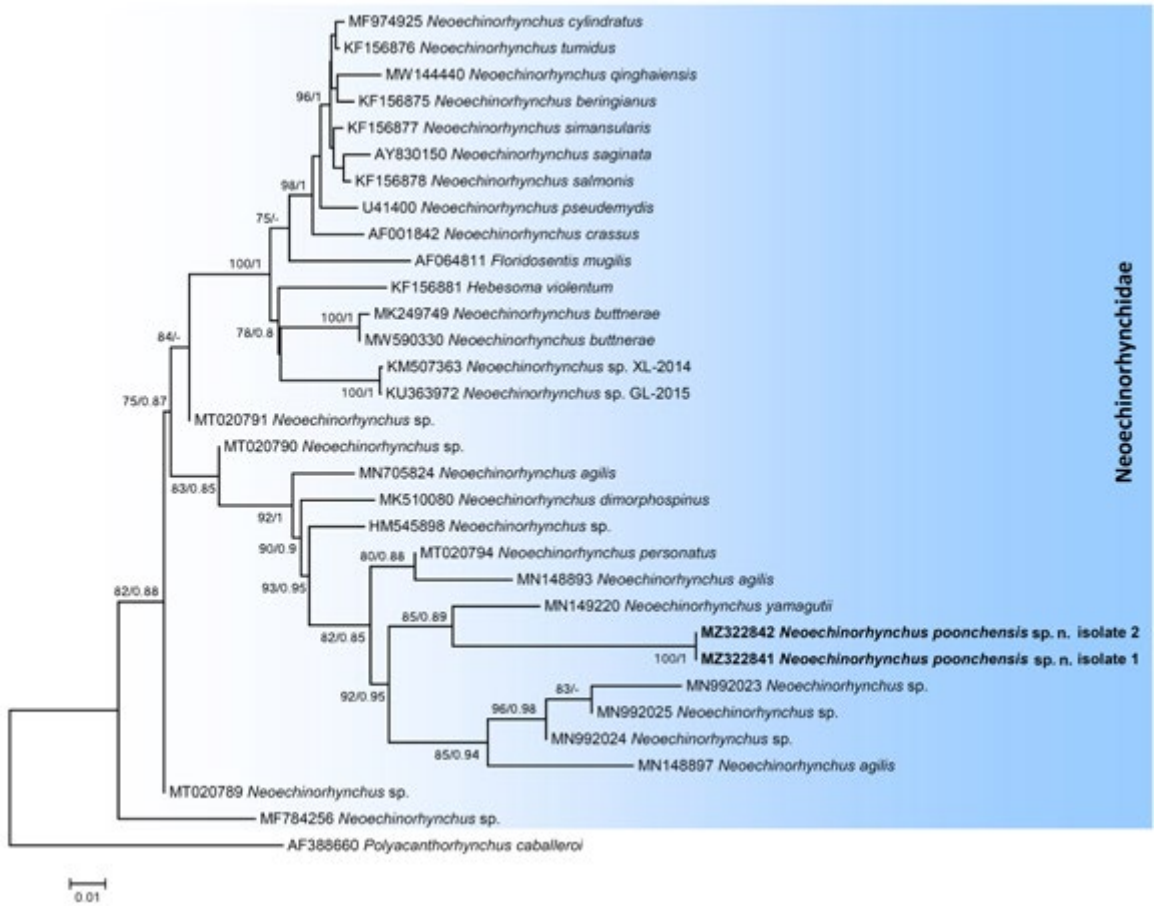

Fig. 4. Maximum likelihood phylogenetic analysis based on 18S rDNA sequences for *Neoechinorhynchus poonchensis* sp. n. and other related sequences available from GenBank for representatives of the Neoechinorhynchidae. Nodal supports for ML and BI analyses are indicated as bootstrap values/posterior probabilities. Nodes unsupported by BI are marked with a hyphen. The new species is in bold. The scale bar indicates the expected number of substitutions per site.

Table 2. Chemical composition of anterior hook, at different locations, of *Neoechinorhynchus poonchensis* n. sp. from the intestinal tract of *Schizothorax richardsonii* (Gray) in India.

Element*	Whole hook	Hook base		Hook tip	
		Centre	Edge	Centre	Edge
Magnesium (Mg)	0.88	0.23	0.19	0.23	0.15
Sodium (Na)	3.82	0.84	0.61	0.35	0.23
Phosphorus (P)	0.62	2.23	2.80	1.15	0.80
Sulfur (S)	4.84	4.80	6.76	7.39	8.40
Calcium (Ca)	1.29	1.77	2.25	0.81	0.74

*Palladium (Pd) and gold (Au) were used to count the specimens and the gallium for the cross cut of the hooks. These and other elements (C, O, N) common in organic matter are omitted. Data are reported in weight (WT%).

divergence was observed with *Neoechinorhynchus agilis* (Rudolphi, 1819) from Spain (Fig. 4).

The *cox1* phylogenetic tree inferred from ML and BI analyses shows that *N. poonchensis* is nested in an independent clade with relatively high bootstrap and posterior probability support values, as same as the tree generated using 18S rDNA analysis (Fig. 5). The isolates of *N. poonchensis* obtained in this study are sister to *Neoechinorhynchus panucensis* Salgado-Maldonado, 2013 (MK089513), *Neoechinorhynchus brentnickoli* Monks, Pulido-Flores et Violante-Gonzalez, 2011 (MG870922) and three unidentified species of *Neoechinorhynchus* sp. (MG870939, MG870943, MG870945), all from Mexico (Fig. 5). The *cox1* genetic divergence among the above species with *N. poonchensis* was with *N. panucensis* (0.56%), *N. brentnickoli* (0.80%) and three *Neoechinorhynchus* spp. (MG870939, MG870943, MG870945) (0.95–1.00%).

DISCUSSION

The type host of the new species, *Schizothorax richardsonii*, is native to the Himalayan region of India, Bhutan, Nepal, Pakistan, and Afghanistan where it is found in mountain rivers among rocks. Our specimens were collected in January just before the host breeding season in April and May when the feeding activity deceases. The common snow trout is threatened by overfishing, damming and introduction of exotic fish, especially salmonids (Froese and Pauly 2006, Chen and Yang 2008). *Schizothorax richardsonii* is a bottom feeder with ventral mouth and hard papillated palate designed for scrapping algae and diatoms from rocks. In various torrential Himalaya streams, adult fish feed primarily on phytoplankton (diatoms, green and blue-green algae) (85–87%) followed by detritus (8%) and sand (5–6%) (Shekhar et al. 1993, Sharma et al. 2018) but juveniles feed upon aquatic insects and their larvae (Sharma et al. 2018). In Telbal and Sindh streams of Kashmir,

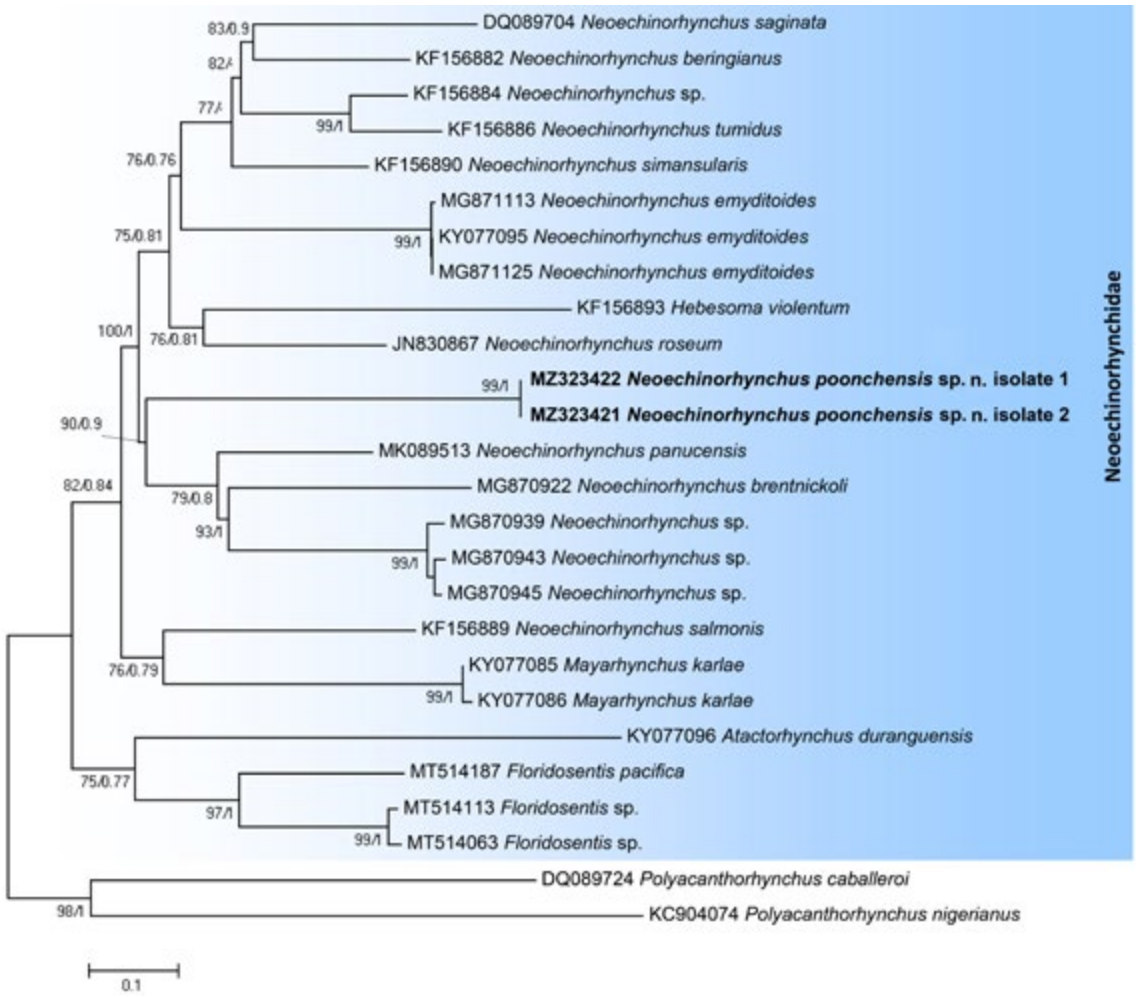

Fig. 5. Phylogenetic tree inferred from cytochrome oxidase subunit 1 (*cox1*) sequences including those from *Neoechinorhynchus poonchensis* sp. n. and closely related taxa. Numbers at the nodes are shown as bootstrap values/posterior probabilities. Nodes unsupported by BI are marked with a hyphen. The new species is in bold. The scale bar indicates the expected number of substitutions per site.

nearer to our collection locality, its diet was reported to include 75% plant matter and 25% animal matter (Mir 1986–1987). The diet profile of *S. poonchensis* in our Jammu and Kashmir collection site must somehow accommodated an intermediate host for the reported infections to take place.

Neoechinorhynchus poonchensis sp. n. stands out among all other species of the subgenus *Neoechinorhynchus* in species with PRS that we have studied, except for *Neoechinorhynchus ascus* Amin, Ha et Ha, 2011 and *Neoechinorhynchus ampullata* Amin, Ha et Ha, 2011 from Vietnam by having two dissimilar para–receptacle structures (PRS), a ventral one inserting near the posterior end of the receptacle and an additional shorter dorsal one inserting at about the middle of the receptacle. In *N. ascus* and *N. ampullata*, the posterior end of the receptacle is supplied with accessory ampulla-like sacs for additional hydrostatic functions (Amin et al. 2011a) lacking in *N. poonchensis*. Other species of *Neoechinorhynchus*, with the usual single ventral PRS, include *Neoechinorhynchus qatarensis* Amin, Saoud et Alkuwari, 2002 from the Arabian Gulf (Amin et al. 2002) and *Neoechinorhynchus johnii* Yamaguti, 1939 from Vietnam (Amin et al. 2019a).

Other species in different genera of acanthocephalans with single-walled proboscis receptacle also have single long ventral PRS. Examples include *Acanthogyrus* (*Acanthosentis*) *parareceptaclis* Amin, 2005 (Quadrigyridae) from Japan (Amin 2005), *Intraproboscis sanghae* Amin, Heckmann, Sist et Basso, 2021 (Gigantorhynchidae) from Central Africa (Amin et al. 2021a), *Pallisentis* (*Pallisentis*) *nandai* Sarkar, 1953 (Quadrigyridae) from India (Amin et al. 2021b), and *Tenuisentis niloticus* (Meyer, 1932) (Tenuisentidae) from Burkina Faso (Amin et al. 2016). In *Acanthogyrus* (*Acanthosentis*) *fusiformis* Amin, Chaudhary, Heckmann, Ha et Singh, 2019, there are two long similar PRS inserting at the posterior end of the receptacle (Amin et al. 2019b).

Most species of *Neoechinorhynchus* were described before the PRS was first recognised in 2002. We have examined the descriptions (and figures) of available species in Amin's (2002) key to 88 species of *Neoechinorhynchus* but could not track clear evidence of PRS. Undoubtedly, other "older" species may have PRS but that will remain unknown because early observers may have missed them or did not know what to look for, and this structure was never reported. We have no access to the type material of all

Table 3. Acanthocephalan species included in the 18S rDNA and mt *cox1* phylogenetic analyses.

Species	Host	Location	GenBank ID		Reference
			18S rDNA	mt *cox1*	
Genus: *Neoechinorhynchus* Stiles et Hassall, 1905					
Neoechinorhynchus agilis	*Mugil cephalus*	Australia	MN705824	-	Huston et al. 2020
Neoechinorhynchus agilis	*Chelon labrosus*	Spain	MN148893, MN148897	-	Sarabeev et al. 2020
Neoechinorhynchus beringianus	*Pungitius pungitius*	Russia	KF156875	KF156882	Malyarchuk et al. 2014
Neoechinorhynchus brentnickoli	*Dormitator latifrons*	Mexico	-	MG870922	Pinacho-Pinacho et al. 2018
Neoechinorhynchus buttnerae	-	Brazil	MK249749	-	Souza and Benavides 2018†
Neoechinorhynchus buttnerae	-	Brazil	MW590330	-	Soares et al. 2021†
Neoechinorhynchus crassus	-	USA	AF001842	-	Near et al. 1998
Neoechinorhynchus cylindratus	*Micropterus salmoides*	USA	MF974925	-	Blubaugh and Gauthier 2018†
Neoechinorhynchus dimorphospinus	*Liza subviridis*	Thailand	MK510080	-	Amin et al. 2019d
Neoechinorhynchus emyditoides	*Trachemys scripta*	Mexico	-	MG871113, MG871125	Pinacho-Pinacho et al. 2018
Neoechinorhynchus emyditoides	*Trachemys scripta*	Mexico	-	KY077095	Pinacho-Pinacho et al. 2017
Neoechinorhynchus panucensis	*Herichthys cyanoguttatus*	Mexico	-	MK089513	Garcia-Varela and Pinacho-Pinacho 2018
Neoechinorhynchus personatus	*Mugil cephalus*	Tunisis	MT020794	-	Amin et al. 2020b
Neoechinorhynchus ponticus	*Chelon auratus*	Ukraine	MT020789, MT020790, MT020791	-	Amin et al. 2020b
Neoechinorhynchus pseudemydis	-	USA	NPU41400	-	Near et al. 1998
Neoechinorhynchus qinghaiensis	-	China	MW144440	-	Pan 2020†
Neoechinorhynchus roseum	*Citharichthys gilberti*	Mexico	-	JN830867	Pinacho-Pinacho et al. 2012
Neoechinorhynchus saginata	-	USA	AY830150	-	Garcia-Varela and Nadler 2005
Neoechinorhynchus saginata	-	USA	-	DQ089704	Garcia-Varela and Nadler 2006
Neoechinorhynchus salmonis	*Salvelinus malma*	Russia	KF156878	KF156889	Malyarchuk et al. 2014
Neoechinorhynchus simansularis	*Salvelinus alpinus*	Russia	KF156877	KF156890	Malyarchuk et al. 2014
Neoechinorhynchus sp.	*Sphyraena barracuda*	China	KM507363	-	Liu et al. 2014†
Neoechinorhynchus sp.	*Coregonus nasus*	Russia	-	KF156884	Malyarchuk et al. 2014
Neoechinorhynchus sp.	*Heteropneustes fossilis*	India	MF784256	-	Mukherjee et al. 2018†
Neoechinorhynchus sp.	*Dormitator latifrons*	Mexico	-	MG870939, MG870943, MG870945	Pinacho-Pinacho et al. 2018
Neoechinorhynchus sp.	*Heteropneustes fossilis*	India	MN992024	-	Kaur and Sanil 2020†
Neoechinorhynchus sp.	*Mugil cephalus*	India	MN992023	-	Kaur and Sanil 2020†
Neoechinorhynchus sp.	*Heteropneustes fossilis*	India	MN992025	-	Kaur and Sanil 2020†
Neoechinorhynchus sp.	*Siganus fuscescens*	China	HM545898	-	Wang et al. 2010†
Neoechinorhynchus sp. GL-2015	*Capoeta aculeate*	Iran	KU363972	-	Adel and Dadar 2016†
Neoechinorhynchus tumidus	*Salvelinus alpinus*	Russia	KF156876	KF156886	Malyarchuk et al. 2014
Neoechinorhynchus yamagutii	*Mugil cephalus*	Russia	MN149220	-	Sarabeev et al. 2020
***Mayarhynchus* Pinacho-Pinacho et al. 2017**					
Mayarhynchus karlae	*Thorichthys ellioti*	Mexico	-	KY077085, KY077086	Pinacho-Pinacho et al. 2017
***Atactorhynchus* Chandler 1935**					
Atactrhynchus duranguensis	*Cyprinodon meeki*	Mexico	-	KY077096	Pinacho-Pinacho et al. 2017
Genus: *Floridosentis* Ward, 1953					
Floridosentis mugilis	*Mugil cephalus*	Mexico	AF064811	-	Garcia-Varela et al. 2000
Floridosentis pacifica	*Mugil curema*	Ecuador	-	MT514187	Rosas-Valdez et al. 2020
Floridosentis sp.	*Mugil curema*, *M. cephalus*	Mexico	-	MT514113, MT514063	Rosas-Valdez et al. 2020
Genus: *Hebesoma* Van Cleave, 1928					
Hebesoma violentum	*Perccottus glenii*	Russia	KF156881	KF156893	Malyarchuk et al. 2014
Outgroup					
Polyacanthorhynchus caballeroi	-	Mexico	AF388660	-	Garcia-Varela et al. 2002
Polyacanthorhynchus caballeroi	-	USA	-	DQ089724	Garcia-Varela and Nadler 2006
Polyacanthorhynchus nigerianus	-	India	-	KC904074	Echi et al. 2015

† Unpublished sequences available on the Genbank database only.

species of *Neoechinorhynchus*, *Acanthosentis*, etc. (if they exist) to verify and can only go by existing descriptions.

Micropores

The micropores of *N. poonchensis*, like those reported from other species of the Acanthocephala, are associated with internal crypts and vary in diameter and distribution in different trunk regions corresponding with differential absorption of nutrients. We have reported micropores in a large number of acanthocephalan species (Heckmann et al. 2013) and in a few more since, and demonstrated the tunneling from the tegumental surface into the internal crypts by TEM. Amin et al. (2009) gave a summary of the structural-functional relationship of the micropores in various acanthocephalan species including *Rhadinorhynchus ornatus* Van Cleave, 1918, *Polymorphus minutus* (Goeze, 1782), *Moniliformis moniliformis* (Bremser, 1811), *Macracanthorhynchus hirudinaceus* (Pallas, 1781) and *Sclerocollum rubrimaris* Schmidt et Paperna, 1978.

Wright and Lumsden (1969) and Byram and Fisher (1973) reported that the peripheral canals of the micropores are continuous with canalicular crypts. These crypts appear to "constitute a huge increase in external surface area . . . implicated in nutrient up take." Whitfield (1979) estimated a 44-fold increase at a surface density of 15 invaginations per 1 μm² of *M. moniliformis* tegumental surface. The micropores and the peripheral canal connections to the canaliculi of the inner layer of the tegument were demonstrated by transmission electron micrographs in *Corynosoma strumosum* (Rudolphi, 1802) from the Caspian seal *Pusa caspica* (Gmelin) in the Caspian Sea (figs. 19, 20 of Amin et al. 2011b) and in *Neoechinorhynchus personatus*

from *Mugil cephalus* Linnaeus in Tunisia (figs. 26, 29, 30 in Amin et al. 2020b).

Para-receptacle structures

Normally, the PRS insert anteriorly in the body wall near the neck and posteriorly at the posterior end of the receptacle, especially on the ventral side. The presence of the PRS in eoacanthocephalans with weak single proboscis receptacle wall was first demonstrated in *N. qatarensis* by Amin et al. (2002) and had since been reported in other species of *Neoechinorhynchus* and *Acanthogyrus* Verma et Datta, 1929 reviewed in part in Amin et al. (2011a). It is reported here in its dual forms, the long ventral and the short dorsal PRS forms, in another species of *Neoechinorhynchus* in a mountain stream in the Jammu-Kashmir region of India. This dual PRS form has been found only twice previously in two marine species of *Neoechinorhynchus* in Vietnam: *N. ascus* and *N. ampullata* (see Amin et al. 2011a). In the description of the PRS, Amin (2002) and Amin et al. (2007) proposed that it may regulate the hydrostatic pressure in the receptacle to facilitate the retraction and eversion of the proboscis. Other genera of acanthocephalans with weak single-wall proboscis receptacle, including *Intraproboscis*, *Pallisentis*, and *Tenuisentis* (see Amin et al. 2016, 2021a,b, respectively), have also been found to have PRS, for the same reasons, which may represent a case of parallel evolution.

Energy Dispersive X-ray Analysis (EDXA)

Our studies of acanthocephalan worms have usually involved X-ray scans (EDXA) of FIB-sectioned hooks and spines (Heckmann 2006, Heckmann et al. 2007, 2012b, Standing and Heckmann 2014). Hooks and spines are evaluated for chemical ions with sulfur (S), calcium (Ca) and phosphorus (P) being the prominent elements. Sulfur is usually seen at the outer edge of large hooks and calcium and phosphorus are major ions in the base and middle of hooks where tension and strength are paramount for hook function. Large hooks play a major role for host tissue attachment.

Results of the X-ray analysis of the FIB-sectioned hooks (dual beam SEM) of *N. poonchensis* show differential composition and distribution of metals in different hook parts characteristic of that species. The edge of the hook tips of *N. poonchensis* showed the highest level of sulfur (8.4%) and lowest levels of calcium (0.74%) and phosphorus 0.8%) while the edge of the hook base had highest level of calcium (2.3%) and phosphorus (2.8%) (Table 2).

These levels are considerably lower than those observed in other species of acanthocephalans. For instance, *Cavisoma magnum* (Southwell, 1927) from *Mugil cephalus* in the Arabian Sea has a similar pattern but considerably higher levels of sulfur in hook tips (43.5 wt. %) and edges (27.5 wt. %) (Amin et al. 2018). This element (sulfur) is part of the prominent outer layer of most acanthocephalan hooks and is a major contributor of the hardening process of this attachment structure. Our results are comparable to those of mammalian teeth enamel. The centre and base of hooks of the same worms had negligible sulfur levels and contained mostly phosphorus and calcium, the two other essential elements for hook structure (Amin et al. 2018). The chemical elements present in the hooks are typical for acanthocephalans (Heckmann et al. 2007, 2012b). The high Sulfur content shows up in the outer edge of X-ray analysis of hooks (Amin et al. 2018, table 4, 5). The hook centre in mid cuts has a different chemical profile than the cortical layer.

X-ray scan analysis provides insight into the hardened components, e.g., calcium, sulfur and phosphorus, of acanthocephalan hooks. The EDXA appears to be species specific, as in finger prints. For example, EDXA is shown to have significant diagnostic value in acanthocephalan systematics. For example, *Moniliformis cryptosaudi* Amin, Heckmann, Sharifdini et Albayati, 2019 from Iraq is morphologically identical to *Moniliformis saudi* Amin, Heckmann, Mohammed et Evans, 2016 from Saudi Arabia, and it was erected based primarily on its distinctly different EDXA pattern (Amin et al. 2019d) as a cryptic species. Our methodology for the detection of the chemical profile of hooks in the Acanthocephala has also been used in other parasitic groups including the Monogenea (Rubtsova et al. 2018, Rubtsova and Heckmann 2019) and Cestoda (Rubtsova and Heckmann 2020).

The biological significance of EDXA as a diagnostic tool is exemplified by the observation that populations of an acanthocephalan species will consistently have similar EDXA spectra irrespective of host species or geography, even though comparative morphometrics of different populations of the same species usually vary with host species and geography (Amin and Redlin 1980, Amin and Dailey 1998). The taxonomic identity of species is deep-seated at the genetic level, which is expressed by the organism's morphology and biochemistry as revealed, in part, by its elemental spectra. In discussing the EDXA of *N. personatus* from *M. cephalus*, Amin et al. (2020b) noted that "The anterior and posterior hooks of our *N. personatus* in the Mediterranean and Black Sea had comparable biochemical profiles."

Erman and Korkut (2011) measured concentrations of 49 different inorganic elements by EDXRF (Energy Dispersive X-Ray Fluorescence spectrometry) in two species of *Agabus* (*A. nebulosus*, *A. conspersus*) (Dytiscidae), collected from the same locality (Adana Province, Turkey). Mn concentration was shown to be significantly different between the two species. Because the two species were collected in the same locality, Erman and Korkut (2011) concluded that "it is unlikely that these differences are due to physiochemical parameters in their habitats (but) instead …. elemental differences may be driven by genetic and biochemical characteristics between the species." Similarly, *Rhadinorhynchus hiansi* Soota et Bhattacharya, 1981 and *Rhadinorhynchus laterospinosus* Amin, Heckmann et Ha, 2011 from the Pacific coast localities of Vietnam show characteristically different EDXA spectra. For instance, the level of phosphorus, sulfur, and calcium in the large anterior hook of *R. hiansi* was 21.2%, 0.46%, and 46.0%, respectively (Amin et al. 2020a), compared to 0.87%, 15.4%, and 2.04% in *R. laterospinosus* in the same hooks Amin et al. 2019c).

Metal analysis of hooks has become the diagnostic standard since hooks have the highest level of elements compared to the mid- and posterior trunk regions of the acanthocephalan body (Heckmann et al. 2012a). Specifically, the sulfur content in the proboscis is paramount in the composition of disulfide bonds in the thiol groups for cysteine and cystine of the polymerised protein molecules (Stedman 2005). Protein synthesis occurs in two stages, transcription and translation by transferring of genetic instructions in the nuclear DNA to mRNA in the ribosomes followed by post-translational events such as protein folding and proteolysis (Stedman 2005).

The formed disulfide bonds are direct by-products of the DNA-based process of protein synthesis which makes up the identity of a biological species. Accordingly, the level of sulfur, in our EDXA profiles will indicate the number of sulfur bonds which along with the levels of calcium phosphates, will characterise the identity of a species based on its nuclear DNA personality. Differences in chemical compositions probably indicate differences in allele expression. The DNA generated sulphide bonds evident in our EDXA profiles have an important role in the stability and rigid nature of the protein accounting for the high sulfur content of the proboscis (Heckmann et al. 2012a). The above processes explain the observed species-specific nature of EDXA profiles noted in our many findings.

Molecular analyses

Within the acanthocephalans, *Neoechinorhynchus* is one of the richest genera with more than 100 species described worldwide (Amin 2013, Pinacho-Pinacho et al. 2014, Garcia-Varela and Pinacho-Pinacho 2018, Amin et al. 2019a). Taxonomic relationships within the acanthocephalans in India is a challenge due to scarcity of molecular data, less satisfactory morphological descriptions lack of expertise with many species described in local journals without peer-review. Various species of *Neoechinorhynchus* are reported from India on the basis of morphological data (Amin 2013). If we focused on molecular data, only four 18S rDNA and three ITS region sequences are available from India on the GenBank database. This points out to the lack of molecular sequences from Indian subcontinent despite the fact that this is the most diverse group in Acanthocephala.

This is the first report of molecular data for any species of *Neoechinorhynchus* from the Jammu and Kashmir, India. Therefore, this study is important for future studies from India regarding *Neoechinorhynchus* and for molecular comparisons. In the present study, ML and BI trees were generated with 18S rDNA and *cox1* congruously indicate that the genus *Neoechinorhynchus* shows paraphyly as also observed by other studies (Pinacho-Pinacho et al. 2017, Garcia-Varela and Pinacho-Pinacho 2018, Amin et al. 2019a). The isolates of species investigated in the current study as *N. poonchensis* in both trees were clustered within a separate lineage within a clade formed by three other 18S rDNA sequences of *Neoechinorhynchus* from southern region of India. No *cox1* sequence is available from India for any species of *Neoechinorhynchus*. Our phylogenetic trees inferred using two molecular markers reveal the genus as paraphyletic. We are suggesting that the addition of molecular data on other species of *Neoechinorhynchus* from India should be generated to understand the taxonomy of acanthocephalans as this group still has problems regarding the taxonomic arrangement of previously described species.

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