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The feeding process of the molluscivorous cone snail *Conus araneosus nicobaricus* Hwass, 1792

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ABSTRACT

The predatory marine gastropod *Conus araneosus nicobaricus* Hwass, 1792 of the family Conidae has been known to prey on gastropods. The prey species so far documented are columbellid and neretid gastropods. Nevertheless, to our knowledge, the feeding process of this species has never been reported. Herein, the prey capture and feeding of *C. a. nicobaricus* in the laboratory condition is described in detail. This is the first report of confamilial predation in *C. a. nicobaricus*. In addition, a detailed account on the role of proboscis, rhynchodaeum, arrangement of teeth within the radular sac and the tooth morphology which is the major weapon of the cone snail to hunt the prey is provided.

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1. Introduction

Conidae is a species-rich family of predatory marine gastropods with approximately 800 extant species (MolluscaBase eds., 2023). Conidae species vary widely in life history, habitat use and ecological attributes, especially feeding ecology (Duda et al. 2001). Most species in the family are known to prey on three general prey types: fishes, gastropods and worms (Franklin et al. 2009). However, individual species are prey type specific (Kohn, 1959, 1968) with few exceptions. Exceptions include *Californiconus californicus* Reeve, 1844 which feeds on fishes, molluscs, polychaetes, cephalopods and amphipods (Kohn, 1966); *Conus bullatus* Linnaeus, 1758 which feeds on both fishes and molluscs (McDowall, 1974); and *Conus eburneus* Hwass in Bruguière, 1792 and *Conus tessulatus* Born, 1778 which have been observed to feed on worms and fishes (Kohn and Nybakken, 1975; Reichelt and Kohn, 1985). Worm-eating species are reported to prey on sedentary polychaetes, errant polychaetes and/or hemichordates (Duda et al. 2001). Nevertheless, very few studies have reported prey types of molluscivorous species (Kohn and Nybakken, 1975; Duda et al. 2001; Kantor, 2007).

Conus araneosus nicobaricus Hwass, 1792 occurs only in the Andaman and Nicobar Islands and Moluccas to Philippines (Röckel et al. 1995). This species has an unusual significance due to its limited or discontinuous distribution (Röckel et al. 1995) in the Indian Ocean and its promising peptide toxin properties (Franklin et al. 2015). It lives in shallow intertidal and subtidal flats of depths almost up to 20 m, generally on sand substrates (Röckel et al. 1995). *Conus araneosus* possesses a species-specific radular tooth structure that suggests a molluscivorous mode of feeding (Nishi and Kohn, 1999; Franklin et al. 2007). Hitherto, the prey species were identified as columbellid snails, probably *Pyrene testudinaria* Link, 1807, which was determined based on radulae and other contents from the alimentary tract of a specimen examined by Kohn (1978), and neretid gastropods (Franklin et al. 2007). However, the feeding process of *C. a. nicobaricus* has never been reported.

Feeding in molluscivorous cone snails involves the use of the 1) proboscis, to protrude, aim and to thrust the radula filled with venom; 2) rhynchodaeum, that envelops the proboscis and expands to engulf the prey; 3) radular sac, to produce and store radular teeth and 4) radular teeth which are detachable spear-shaped hollow structures that are forcefully discharged from the proboscis to paralyse the prey (Kohn and Hunter, 2001; Kohn, 2003). This paper describes prey capture and feeding by *C. a. nicobaricus* as observed in the laboratory. This is the first report of confamilial predation in *C. a. nicobaricus.* The radular sac and teeth are described and illustrated. The likely transport of teeth inside the radular sac before injection and functions of proboscis and rhynchodaeum (also called the 'proboscis sheath' or 'false mouth' (Kohn and Hunter, 2001) are discussed in detail. Finally, because most injection syringes are composed of non-degradable metals and plastics, bio-mimicking the natural syringe of cone snails into a viable injection syringe for human use may open up new areas of research and may reduce medical waste or pollution. Therefore, a preliminary analysis was performed to quantify the elemental composition of radular teeth.

2. Materials and Methods

2.1. Feeding observations

Two specimens of *Conus a. nicobaricus* of shell lengths (SL) 52 mm and 60 mm were collected from the intertidal sand of Aberdeen Bay, Andaman Sea on 8th October, 2019. Shell length (SL) and shell width (SW) of specimens were recorded to the nearest millimeter. Living specimens were kept in an aquarium for five days prior to observations of feeding. Specimens of different species of snails of the families Cypraeidae, Strombidae, Neritidae and Hydantinidae (i.e., species that were observed during field surveys in similar or nearby habitats where *C. a. nicobaricus* was collected) were offered. Nevertheless, the *C. a. nicobaricus* specimens did not feed on any of these potential prey specimens for four days. On the fifth day, additional cone snail species that were collected from different locations in South Andaman were added to the aquarium, holding the specimens of *C. a. nicobaricus*. These included *Conus coronatus* Gmelin, 1791 (1 specimen; SL 35 mm), *Conus flavidus* Lamarck, 1810 (2 specimens; SL 48 mm and 52 mm), and *Conus zonatus* Hwass in Bruguière, 1792 (1 specimen; SL 60 mm). The tank was cleaned and fresh filtered seawater was pumped directly from the bay into the tank before we placed the snails in the aquarium. After introducing these *Conus* specimens, the largest specimen of *C. a. nicobaricus* (SL 60 mm) became quite active and a feeding bout on one of the introduced *Conus* specimens was observed.

2.2. Preparation of teeth for optical microscopy

Radular sacs were removed from the body cavity and stored in 70% ethanol. Mature radular teeth were taken from the short arm of the radular sac using a thin brush for morphometric analysis. The teeth were cleaned in dilute sodium hypochlorite solution (20%), followed by double distilled water. To observe the arrangement of teeth inside the radular sac, dilute sodium hypochlorite solution (20%) was added drop by drop onto the sac and frequently observed under microscope until the teeth arrangement was visible. The teeth were mounted in water on glass slides and observed under a compound microscope, as described by Franklin et al. (2007). Tooth lengths were measured with an optical micrometer to the nearest 0.1 mm.

2.3. Preparation of teeth for SEM

Preparation of teeth for scanning electron microscopy (SEM) follows Franklin et al. (2007). In brief, radular teeth were dehydrated in increasing ethanol concentrations from 10% to absolute ethanol and then air-dried. With the help of a sharp tipped needle, the teeth were subsequently fixed on to double-sided tape fixed to SEM stubs. The SEM stubs were then coated with gold and observed on a JEOL JSM-840 scanning electron microscope.

2.4. Elemental composition of radular tooth

Quantification of basic elements present in radular teeth was determined using a Quanta Low vacuum/ environmental scanning electron microscope equipped (ESEM) coupled to an Energy Dispersive Spectroscopy (EDS) detector of EDAX system that detects x-rays emitted from a sample during electron imaging and that is controlled by means of a user interface (UI) program, called Genesis Software Version 3.6. More than 10 teeth were analysed for consistent results. This allows sample characterization on unpolished coating-free samples. The analyses were carried out under a pressure value of 90 Pa and 20 kV as the accelerating voltage. The spectra obtained from ESEM revealed the presence of non-metallic, halogen, alkali, and alkaline elements. Different parts of the radular tooth (e.g., tooth apex, middle shaft and tooth base) were examined.

2.5. Preparation of internal organs for histology

The parts of the organs to be sectioned were dissected out and fixed in buffered formalin, embedded in paraffin, sectioned at 6 µm, and stained with haematoxylin and eosin (Ross and Pawlina, 2006). Permanent slides were prepared and observed under a microscope. Photographs of sections were taken using a charged coupled device (CCD) camera attached to the Olympus SZX16 Zoom Stereo Microscope.

3. Results and Discussion

3.1. Feeding observations

After other cone snail species were placed in the aquarium (see section 2.1), the largest *Conus araneosus nicobaricus* individual became very active (Fig. 1A), moving from one end to the other. Although most cone snails are believed to be active at night (Kohn and Hunter, 2001), we observed this feeding behaviour during the day (15:00 hrs.). There was no sand on the bottom of the tank, so the base was smooth and the snails moved relatively quickly. *Conus a. nicobaricus* extended its siphon as it first approached *C. flavidus* (which was similar to its size), but then moved quickly away from this individual. At that time, *C. coronatus* crossed in front of *C. a. nicobaricus* and came in contact with its siphon. The siphon extended further and approached towards *C. coronatus*. The tip of the siphon of *C. a. nicobaricus* has a thin yellow line followed by a narrow white stripe (background colour) and a broad black band followed by white (background colour), then sparse to densely mottled with brown; the interior of the siphon is white (Fig. 1B; for clarity shown from a different specimen).

After six minutes (15:06 hrs.), the siphon and proboscis were extended and lifted up by the animal, extending forward its foot completely as it was apparently attempting to probe the prey. Sometimes, the proboscis was observed to extend approximately 1.5 times the length of the shell of the specimen. The proboscis was deep orange in colour. The proboscis injected the radula above the foot region of the prey after an additional four minutes (15:10 hrs.). Immediately, the foot of *C. coronatus* was drawn back into its shell and the specimen stopped moving. Then, *C. a. nicobaricus* withdrew its proboscis and its rhynchodaeum expanded slowly (15:12 hrs.). In the case of worm-eating cone snails, the proboscis tip retains its grip on the expanded proximal end of the tooth and the tooth and proboscis act analogously to a harpoon and its line to pull the prey into the expanded rhynchodaeum (Kohn, 1998; Kohn and Hunter, 2001). However, in our observation, the proboscis was withdrawn immediately after injection of the tooth. Although, Kohn et al. (1999) have reported multiple injections of tooth (2 to 6) into prey by molluscivorous cone snails, we observed only one injection.

After the snail's rhynchodaeum extended, the slender eye stalks on either side of the movable rhynchodaeum extended and tentacles were clearly visible. The tentacles have black lines on both sides on a white background, distally round tipped with pair of eyes imbedded as a black dot just below the tip; the tips are tinged with yellowish-beige (Fig. 1C; for clarity shown from a different specimen).The distal end of the siphon embraced the shell of the prey (i.e., held the prey by making a hook-like curve with its siphon) and pulled it towards the rhynchodaeum. Eventually, the rhynchodaeum expanded to a funnel shape and appeared to be attempting to hold the shell. The rhynchodaeum, anterior region of the foot, and siphon acted together at the same time to move the prey (15:13 hrs.), so that it's apertural side was directed towards the rhynchodaeum of the predator. As soon as the aperture was apparently in an accessible position, the distal

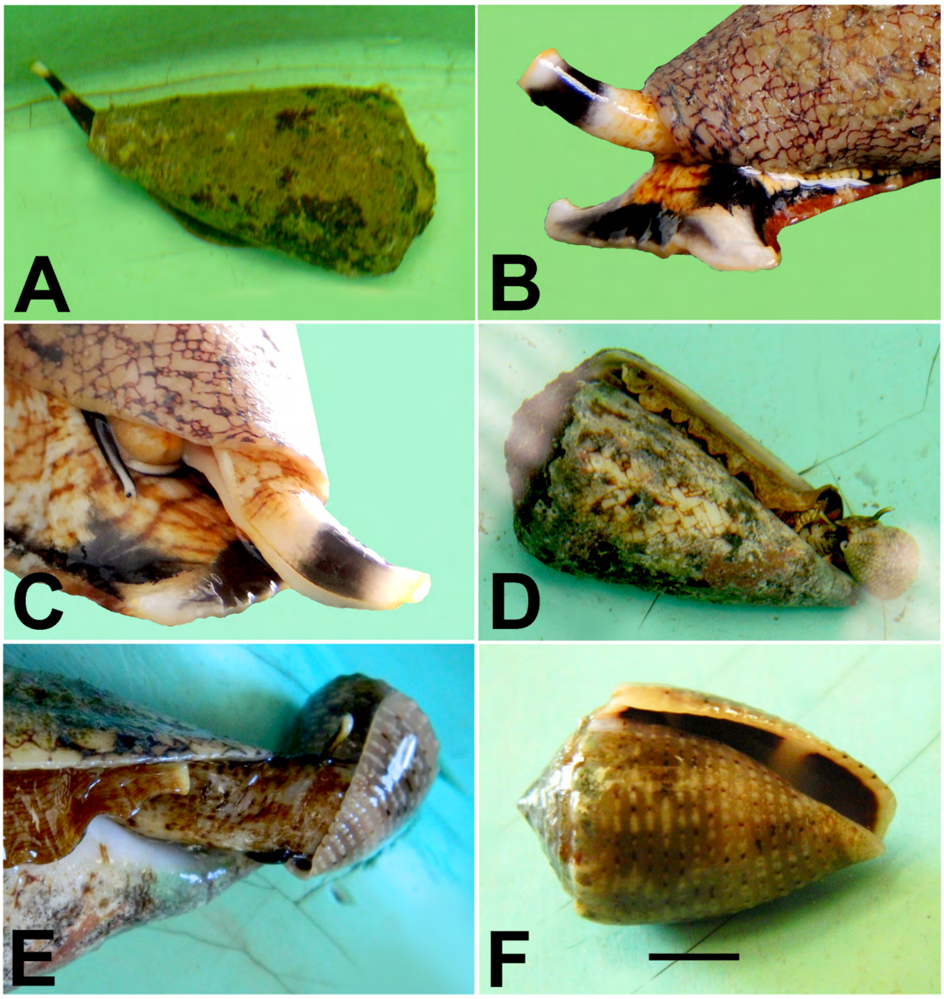

Fig. 1. *Conus araneosus nicobaricus* feeding on *Conus coronatus;* **A**. *C. a. nicobaricus* active in tank, **B**. Pattern of siphon in *C. a. nicobaricus*, **C.** Pattern of tentacles and eyes in *C. a. nicobaricus*, **D.** Entry of rhynchodaeum into *C. coronatus* aperture, **E.** Close-up view of rhynchodaeum in the prey and **F.** Empty shell of *C. coronatus* (prey). Scale: **F.** 10 mm.

end of rhynchodaeum became flat and inserted into the aperture of the prey (Fig. 1D; 15:15 hrs.). After the insertion of the rhynchodaeum, *C. a. nicobaricus* moved upwards slightly (1.5 inches) along the side of the tank and then fell down without detaching from the prey. At this point, the apertural side of *C. a. nicobaricus* was clearly visible with part of its rhynchodaeum inside the shell of *C. coronatus*.

Conus a. nicobaricus remained immobile with its rhynchodaeum inside the prey (Fig.1E) for approximately 20 minutes upon which it had apparently swallowed the entire flesh of *C. coronatus* without leaving any tissue (15:35 hrs.) inside the shell (Fig. 1F), presumably by attaching the rhynchodaeum firmly to draw in the flesh. In comparison, the ingestion time of a prey of similar size (30 to 50 mm) by a fish-eating cone snail, *Conus geographus* Linnaeus, 1758, was reported to be 10 seconds to 1 minute (Johnson and Stablum, 1970). During the observation, we did not disturb any snails inside the aquarium. After feeding, *Conus a. nicobaricus* was active in the tank.

3.2. Radular sac and teeth arrangement

The radular sheath or sac is ‚L' shaped with a long and a short arm (Fig. 2A). The short arm opens into the pharynx just anterior to the opening of the venom duct. The other end of the short arm has a pouch called the ligament sac as it houses the ligaments that are attached to the bases of teeth. The long arm is slightly curved and ends blindly. The teeth in the short arm were oriented along its axis with their tips pointing towards the opening of the sac, while the long arm has teeth arranged in two rows with the apex of teeth pointing towards the blind end of the sac. The walls of the short arm of the radular sac are thicker than those of the long arm.

The cross section across the long arm (Fig. 3) revealed the presence of connective tissue (Fig. 3A), smooth muscle fibers and a thin epithelial lining at the lumen of sac. The teeth are arranged in a horseshoe pattern, in which the lumen of the teeth has a gradual increase in size from the ends to the midpoint (Fig. 3B). The increase in lumen size was due to the section that cut at different part of the teeth arranged inside the sac as a chain clustered with each other. It is believed that the tooth develops from the blind end of the long arm. Each tooth has a thin layer of a cast-like enfold, in which it develops. Mature teeth move towards

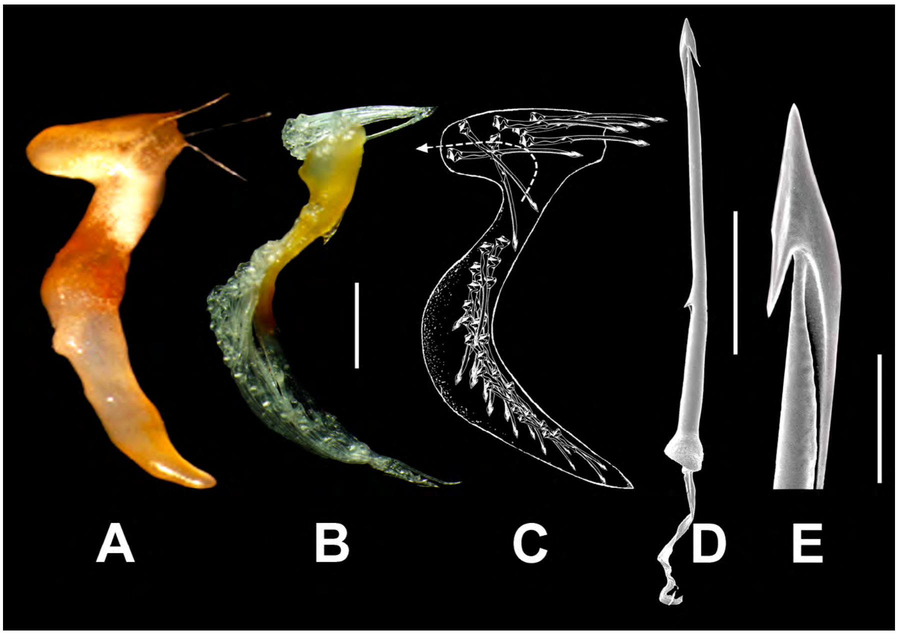

Fig. 2. Radular sac and radular teeth of *Conus araneosus nicobaricus;* **A.** Radular sac showing short and long arm, **B.** Serial arrangement of radular teeth inside the radular sac, **C.** Illustration shows the likely movement of teeth, **D.** Entire tooth and **E.** Tooth apex enlarged. Scale: **A, B** and **C.** 1 mm; **D.** 500 µm; **E.** 100 µm.

the short arm where they are stored. We did not observe any structural differences in the teeth present in the long arm. Most teeth had a ligament attached to them in the long arm. The teeth arrangement was observed by dissolving the outer sheath of the sac gradually (Fig 2B; Fig 3C). Two teeth were arranged together in a row, and the chain of teeth had 16 to 18 rows.

The tooth chain extends from the long to short arm. Before it reaches the collar region, the base of the mature tooth turns in such a way so that the tooth base enters the ligament sac. As the base moves inside the ligament sac, the apex of the tooth hangs free and could move upward to attain a 360˚ rotation so that it is positioned in the short arm and is ready for deployment (Fig. 2C). The attachment of the ligament was previosuly believed to take place in the ligament sac. The present observations show the presence of ligaments in both arms of the radular sac.

3.3. Tooth morphology and elemental composition

The structure of radular teeth of *C. a. nicobaricus* (Fig. 2D) appears to be unique to this species. The tooth apex has one barb and one blade (Fig. 2E) with serrations terminating into a cusp just distal to the centre of the tooth shaft. The terminal knob lacks a spur. Present observations on the radular teeth morphology is consistent with published reports (Nishi and Kohn, 1999; Franklin et al. 2007). A healthy specimen of shell size 79 × 42 mm, with its radular sac measuring 12 mm was observed to have 12 fully formed teeth in the short arm and 32 teeth in the long arm. Usually, a ligament is attached to the base of each tooth. Only one tooth is used at a time. The mechanism is demonstrated in the fish-eating snail *Conus catus* Hwass in Bruguière, 1792, where the biomechanical means of tooth ejection is based on a ballistic prime-and release mechanism, which probably involves contraction of the proboscis muscles to propel the radular tooth into unsuspecting prey (Schulz et al. 2004).

A preliminary elemental quantification of radular teeth revealed non-metallic elements like carbon (35.3 to 39.9%), oxygen (19.6 to 23.1%), and an alkaline element, calcium (33.6 to 35.5%) as the major elemental components of teeth. Alkali elements like sodium (0.2 to 0.6%) and rubidium (0.4 to 0.5%) and other alkaline elements such as magnesium (1.1 to 1.6%) and salts such as chlorine (4.2 to 4.3%) were observed at lower percentages (Fig. 4). Different parts (apex, middle shaft and base) of the radular tooth showed similar patterns with minor variations (see Table 1).

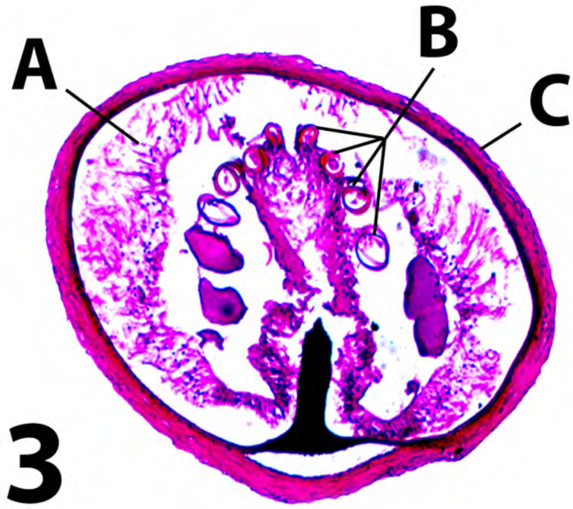

Fig. 3. Transverse section of the long arm of the radular sac of *Conus araneosus nicobaricus*. **A.** Connective tissue, **B.** Radular teeth arranged in a semi-circular fashion, having matured teeth at both ends and **C.** Outer layer of radular sheath

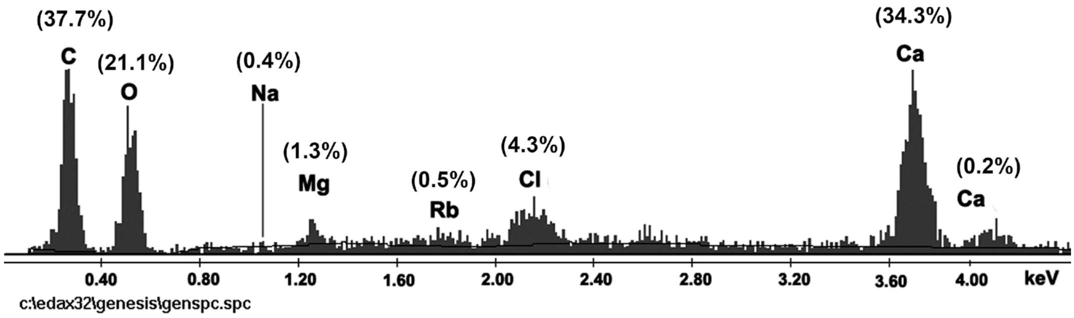

Fig. 4. Energy Dispersive X-Ray Spectroscopy spectrum showing the elemental composition of *Conus araneosus nicobaricus* radular teeth

Table 1. Elemental composition of the radular tooth of *Conus araneosus nicobaricus*

Tooth parts	Elements Wt %							Total (%)
	Carbon	Oxygen	Calcium	Sodium	Rubidium	Magnesium	Chlorine	
Tooth apex	38.5	20.7	34.4	0.6	0.5	1.1	4.2	100
Middle shaft	35.3	23.1	35.5	0.2	0.4	1.2	4.3	100
Tooth base	39.9	19.6	33.6	0.5	0.5	1.6	4.3	100
Average	**37.9**	**21.1**	**34.5**	**0.4**	**0.5**	**1.3**	**4.3**	**100**
Standard deviation	2.4	1.8	1.0	0.2	0.1	0.3	0.1	

3.4. Proboscis

The general structural pattern of the proboscis of *C. a. nicobaricus* is similar to that of other Conidae species. It is a remarkably flexible structure and extends approximately 1.5 times longer than the shell length of the specimens and contracts considerably into a small part of the rhynchocoel. It is assumed that the proboscis provides the necessary positive pressure to mediate the venom ejection (Greene and Kohn, 1989; Kohn and Hunter, 2001). A cross section of the proboscis of *C. a. nicobaricus* has an epidermis (Fig. 5A), haemocoel (Fig. 5B), longitudinal muscles (Fig. 5C), sphincter (Fig. 5D), connective tissue (Fig. 5E), epithelium of the lumen (Fig. 5F) and lumen (Fig. 5F). The fibrous connective tissue maintains the tubular shape without flattening during tooth injection as mentioned by Kohn (1989). The arrangement of circular muscles in the outermost layer and longitudinal muscles in all three layers appears to be shared among almost all members of Conidae. The presence of fluid in the haemocoel acts as a hydrostatic skeleton and also functions in changing the length of the proboscis during prey search (Kohn, 1956). In addition, the presence of telescopic folds in the inner wall was considered by Kantor (2007) as a key feature that allows the proboscis to extend and contract. In exception to other functions, the proboscis also helps to further assay the prey after venom injection (Kantor, 2007). In *Conus a. nicobaricus*, we believe that the presence of longitudinal and circular muscle and helical fibers along with the fluid space mutually act as a hydrostatic skeleton that is similar to the framework of *C. catus* described previously by Greene and Kohn (1989). Several genera of the family Turridae possess a similar structural framework except for a few differences in the haemocoel and the connective tissue (Sysoev and Kantor, 1987; Kantor, 1988).

3.5. Rhynchodaeum

The function of the rhynchodaeum during predation is to engulf and lead the prey into the proboscis. It is thin and wide in the beginning and spreads out into a funnel shape during predation. A cut across the proximal part of the sheath (Fig. 6A) revealed the inner wall with thick circular broad band-like structure (collar) below the tip. The tip ends thin. The rhynchodaeum has a unique framework on its inner wall (Fig. 6B) for its multiple tasks. The inner wall is rough presumably due to multiple and regular folding. Horizontal folding with regular grooves and vertical folding

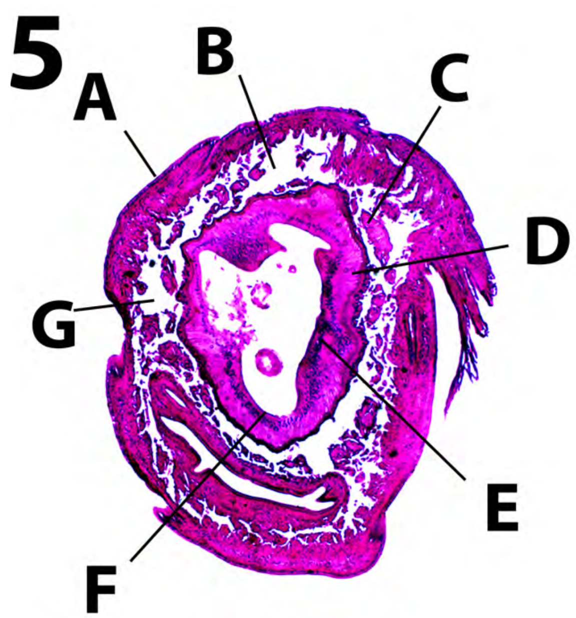

Fig. 5. Transverse section of the *C. a. nicobaricus* proboscis. **A.** Epidermis, **B.** Haemocoel, **C.** Longitudinal muscles, **D.** Sphincter, **E.** Connective tissue, **F.** Epithelium of the lumen and **G.** Lumen.

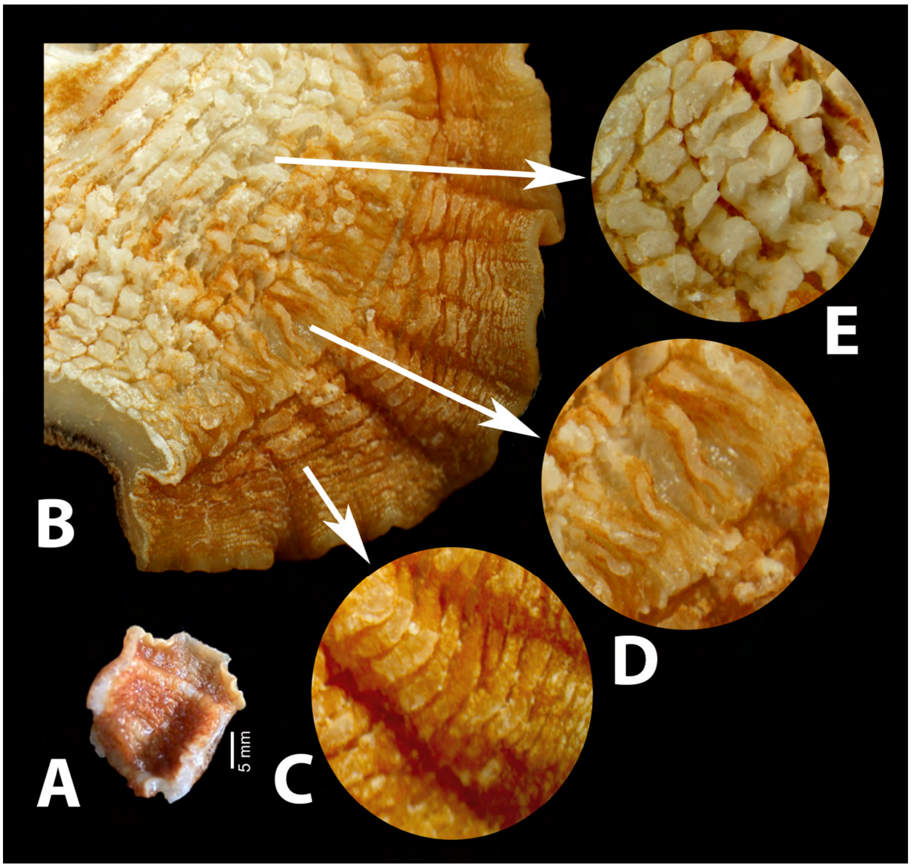

Fig. 6. Rhyncodaeum of *Conus araneosus nicobaricus*. **A.** Inner layer after a cut across the proximal part, **B.**Inner layer enlarged, **C.** Horizontal and vertical foldings, **D.** Sphincter muscles in the collar region, and **E.** Regular pad-like protruding outgrowths. Scale: **A.** 5 mm

in an almost conical shape occupy the space between the tip of proboscis and the collar region (Fig 6C). This structure allows the part to expand or constrict in both sides and to form an elongated funnel shape, reduce it to a tube shape, or constrict it to close. The middle broad folding that occurs in the collar region allows it to expand or constrict in one-way (circular) manner, probably via sphincter muscles (Fig. 6D). The broad band like structure (in the collar region) has been reported earlier from turrids, which is called as `rhynchostomal sphincter` that acts to hold and to facilitate the destruction of prey for digesion without much effort (Fedosov and Kantor, 2008). The purpose of sphincter muscle in the collar region may be to 1) act as a noose to prevent the escape of prey, 2) propel the prey inside and/or 3) crush the prey to fit its size. It also envelops the proboscis. The construction of regular pad-like protruding outgrowths arranged side-ways horizontally on the posterior part might act as a grip to push the prey inside (Fig. 6E).

4. Conclusion

The venom of cone snails has been studied extensively in the past four decades and has yielded a drug called Prialt™ derived from *Conus magus* Linnaeus, 1758 that is currently used to treat chronic pain (Safavi-Hemami et al. 2019). Similarly, the detachable spear-shaped radular teeth used for injecting venom into the prey of cone snails have immense value, if further in-depth research is carried out on 1) how teeth are produced inside the radular sac and 2) if tooth composition could be mimicked in the laboratory to produce a degradable medical tool like an injection syringe useful to mankind.

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