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*Original Article*

# Feeding apparatus, digestive system structure, and gut contents of Priapium fish, *Neostethus lankesteri* Regan 1916

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## Abstract

In this study, we examined the gut contents and morpho-histology of the digestive tract of *Neostethus lankesteri* Regan, 1916 to examine habitat utilization. Thirty individuals of *N. lankesteri* were collected monthly from two sites: Pranburi River estuary (PRE) and Sirinart Rajini Mangrove Ecosystem Learning Center (SRMELC), during the Northeast and Southwest monsoon season. Based on gut contents analysis of *N. lankesteri*, the primary food items were categorized as follows: diatoms, dinoflagellates, other microalgae, and zooplankton. The index of relative importance, IRI, showed that diatoms were a major component followed by zooplankton at the PRE site, whereas zooplankton was a major component followed by diatoms at SRMELC during the two seasons. Moreover, *N. lankesteri* had a superior mouth with canine teeth. The pharyngeal tooth plates were numerous and canine shaped. The intestine coefficient of *N. lankerteri* was 0.55, which is consistent with omnivory. Histology of the digestive tract in *N. lankesteri* showed that they were stomachless, while the intestine consisted of three regions: anterior, middle, and posterior. Collectively, gut content and morpho-histological analyses from our studies indicated that *N. lankesteria* is an omnivore, feeding on multiple trophic levels depending on their availability.

**Keywords**: digestive system, feeding ecology, histology, Priapium fish, Thailand

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## 1. Introduction

The Priapium fish *Neostethus lankesteri*, belonging to family Phallostethidae, is a small, slender body fish that can be commonly found throughout Southeast Asia (Paphavasit, Siriboon, Jaiperm, & Mookui, 2014). The fish is often overlooked because of its small size; however, because of its high abundance, it is possible that this fish plays a key role in linking primary producers and the secondary consumers in its native habitat. Previous literature has tended to suggest that Phallostethids are carnivores, which feed mainly on insects (Villadolid & Manacop, 1934). Additionally, Mok and Munro (1991) reported that copepods are the main food item of *Neostethus bicornis* and *N. lankesteri*. Specially, the study of *N. lankesteri* from Singapore showed that copepods were the main food item based on gut content analysis (Mok & Munro,

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1991), however, this study suffered from low sample size (n=17) and did not consider seasonal variation in the sampling regime. Seasonal variability in diet is expected, as it would reflect the variability in items available that naturally change throughout the year. Furthermore, on a more general level, fish within the same genus and within the same species have been shown to select different prey items in different habitats (Kaifu, Miyazaki, Aoyama, Kimura, & Tsukamoto, 2013). The application of relating the histological structure of the digestive tract to feeding habits in fishes has been performed on other species such as *Puntius stoliczkanus* (Senarat, Yenchum, & Poolprasert, 2013) and *Rastrelliger brachysoma* (Senarat, Kettratad, Jiraungkoorskul, & Kangwanrangsan, 2015) and *Dermogenys pusilla* (Senarat *et al.*, 2020); however, there is no knowledge on the digestive biology of *N. lankesteri*. In this study, the gut contents of *N. lankesteri* sampled during northeast and southwest monsoon seasons in Thailand was investigated, and the fish digestive system structure was examined to provide baseline information on its feeding ecology.

## 2. Materials and Methods

Healthy adult *N. lankesteri* with standard lengths (SL) of 2.53±0.31 (mean±SD) cm were collected by larval trawl from two sites; Pranburi River estuary (PRE) (ST1, 12°24'15.8" N, 099°58'25.6" E, ST2 12°24'21.6" N, 099°58'37.1" E, ST3 12°24'08.5" N, 099°59'00.2" E) and Sirinart Rajini Mangrove Ecosystem Learning Center, SRMELC (ST4, 12°23'43.52" N, 099°58'49.45" E, ST5, 12°23'53.77" N, 099°58'55.98" E, ST6, 12°23'53.52 "N, 099°58'53.0" E) (Figure 1), Thailand during the northeast monsoon (November 2015 – April 2015) and southwest monsoon season (May 2015 – October 2015). Thirty individuals/ station/ month (total random sampling of 2,160 individuals) were collected from six localities. All fish were euthanized by a rapid cooling shock protocol (Wilson, Bunte, & Carty, 2009). The experimental protocol was approved by the Animal Care and Use Committee of Faculty of Science, Chulalongkorn University (Protocol Review No. 1523005).

All specimens were fixed with Davidson's fixative (about 48 hrs) and then transferred to 70% ethanol to perform gut content analysis. After dissecting, all samples of the digestive tract were examined and the intestines were measured to calculate the intestine coefficient (IC). The ratio of intestinal length (LIT) and body length (LS) was calculated by the equation $IC = LIT / LS$. The prey items were identified according to the guidelines of Tomas (1997) and Casanova and Boltovskoy (1999) under Dino Eye Piece AM-423C for attachment of a digital camera. The index of relative importance (IRI) was used to describe the importance of each prey item to fish diet and explain the feeding habits of *N. lankesteri* (Cortés, 1997; Hyslop, 1980). Index of relative importance, $IRI = (\% Ni + \% Vi) \% Oi$; Where, Ni, Vi, and Oi represent percentages of number, volume and frequency of occurrence prey respectively, as described by (Pinkas *et al.*, 1971) and Hyslop (1980) were calculated.

Ten specimens of *N. lankesteri* in Davidson’s fixative were chosen for analysis. These ten fish had a mean SL (±SD) of 2.44 (0.33) cm and were dissected for both digestive tracts under stereomicroscopy. All samples were examined for their gross anatomy and subsequently subjected to standard histological techniques (Presnell & Schreibman, 1997). Histological sections were routinely stained by hematoxylin and eosin (H&E), Masson's trichrome stain, periodic acid Schiff (PAS) and alcian blue pH 2.5 (AB) (Presnell & Schreibman, 1997). The histological observations of the digestive tract and accessory organs of this species were assessed by using a light microscope and were photographed using an Olympus CX31 light microscope mounted with a Canon EOS100 camera. Additionally, ImageJ version 4.9 was used for the analysis of the length of the longitudinal folds among different intestine regions (anterior to posterior intestines).

Analysis of variance (ANOVA) was used to examine the differences of prey composition in each habitat between the northeast and southwest monsoon seasons, and used for examining the differences in the length of the longitudinal folds among different intestinal regions. All of the statistical tests were performed with the software SPSS statistics 22.

## 3. Results and Discussion

### 3.1 Analysis of gut content

The food items of *N. lankesteri* were classified into four groups: diatoms (centric diatoms and pennate diatoms),

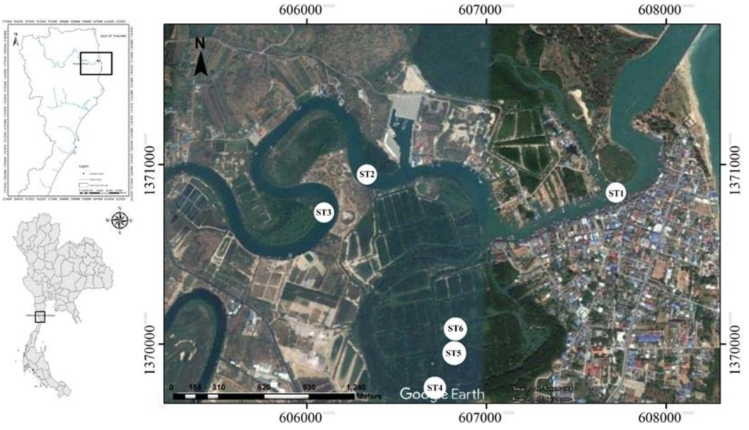


Figure 1. Sample sites of *Neostethus lankesteri* in the Pranburi River Estuary (ST1-ST3) and the Sirinaj Rajini Mangrove Ecosystem Learning Center (ST4-ST6), Pranchuap Khiri Khan Province

algae (*Merismopedia* sp.), dinoflagellates (*Noctiluca* sp.) and zooplankton (Table 1). The type of prey items in the gut contents from the southwest monsoon season were not different from those observed in the northeast monsoon. On the other hand, the amount of prey items in the gut contents of the PRE fish were different from those collected from the SRMELC.

The gut contents of *N. lankesteri* from PRE in both seasons revealed that the major component of the diet were diatoms (approximately 90%IRI) (Table 1). Diatoms were found in high abundance in the PRE during the two sampling periods; approximately 10,000 cells per liter (Figure 2). By the large number of frequencies of occurrence (O) and a smaller number of number (N), the IRI value can be inflated, and cause the %IRI of diatoms to be much higher than the zooplankton. Despite the proportion of IRI of diatoms being highest however the percentage of volume of diatoms in the gut was below that observed in the percent volume of zooplankton (Table 1). In contrast, the diet component of *N. lankesteri* from SRMELC showed that the major prey item was zooplankton (81%IRI; Table 1); copepods contributed more than 62%IRI of the total zooplankton component during the northeast monsoon season. During the southwest monsoon, copepods contributed approximately 38%IRI, which was a major component (52.6%IRI) of the total zooplankton component (Table 1). The diatom density from SRMELC was not significantly different from Pranburi River Estuary. The diatoms in the gut contents were likely from incidental ingestion, which is the case when fish accidentally eat non-target prey during the pursuit of target prey (O'brien, 1987). Incidental ingestion also has been reported in *Centropogon australis*, as a macrophagic carnivore (Bell, Burchmore, & Pollard, 1978). Since it consumed seagrass and algae as minor food items, this suggests that the seagrass and algae are representative of accidental consumption. We hypothesized that diatoms in the gut (Table 1) were due to accidental ingestion, and hence would be higher in the gut contents of fish from the PRE relative to SRMELC because of the high abundance of these non-target prey in the water column of the former site.

## 3.2 Digestive tract morphology

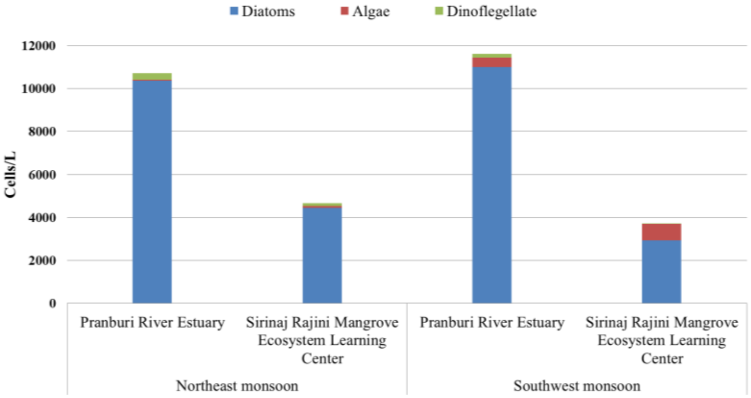
*N. lankesteri* had a superior mouth that is highly protrusible, similar to what has been found in *N. bicornis* (Mok & Munro, 1991). The average width and height of the mouth gape was 1.25±0.02 and 1.55±0.11 mm, respectively. The dimension of zooplankton and phytoplankton (copepods with 0.18±0.08 mm width, 0.58±0.32 mm length and phytoplankton, *Coscinodiscus* spp. (0.23±0.32 mm diameter)) matched with the mouth gape dimension of *N lankesteri* as an optimal prey size (Gerking, 2014). Both prey items were relatively small compared to the mouth gape dimension of *N. lankesteri*. Therefore, the dimension of the prey items support the conclusion reached above that diatoms were accidentally ingested while *N. lankesteri* target copepods and/or other zooplankton as their main prey item(s).

The teeth of *N. lankesteri* are unicuspid, found on the premaxilla (upper jaw) and the dentary (lower jaw). *Neostethus lankesteri* has a row of small teeth in the lower jaw, which are opposed to a row of larger teeth on the upper jaw. The premaxilla bears a series of larger teeth, which are canine-shaped and located at the edge of the snout (Figure 3). This arrangement of teeth is similar to the closely related species *N. bicornis*; Mok and Munro (1991) suggested that the shape of the teeth of *N. lankesteri* and *N. bicornis* were related to feeding behavior which suggests that they fed on small animals. *N. lankesteri* had short gill rakers that varied from 15-18 slits. Short gill rakers are required to pick plankton rather than filter them and, as such, is similar to *N. bicornis*

Table 1. Summary of prey items found in the gut contents of *Neostethus lankesteri*

| | Northeast monsoon | | | | | | Southwest monsoon | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Pranburi River Estuary | | | SRMELC | | | Pranburi River Estuary | | | SRMELC | | |
| | %v | IRI | %IRI | %v | IRI | %IRI | %v | IRI | %IRI | %v | IRI | %IRI |
| Diatoms | 14.6 | 879071.3 | 89.5 | 0.6 | 60839.4 | 18.9 | 11 | 861981.8 | 92.1 | 3.05 | 112976.3 | 47.3 |
| Algae | 0.6 | 592.7 | 0.1 | n/a | n/a | n/a | 0.08 | 592.7 | 0.1 | n/a | n/a | n/a |
| Dinoflagellates | 0.81 | 926.1 | 0.1 | n/a | n/a | n/a | 0.03 | 135.5 | 0 | 0.06 | 29.9 | 0 |
| Zooplankton | 83.9 | 101455.9 | 10.3 | 99.4 | 260840.6 | 81.1 | 88.89 | 73589 | 7.9 | 96.89 | 125597 | 52.6 |
| Copepods | n/a | 35921.8 | 3.7 | n/a | 199669.1 | 62.1 | n/a | 37777.4 | 4.0 | n/a | 90716.2 | 38.0 |
| Mollusk lavae | n/a | 58.9 | 0.0 | n/a | 1031.9 | 0.3 | n/a | 1180.3 | 0.1 | n/a | 549.4 | 0.2 |
| Cirripedia larvae | n/a | 7960.2 | 0.8 | n/a | 8355.7 | 2.6 | n/a | 53.1 | 0.0 | n/a | 2371.9 | 1.0 |
| Nematodes | n/a | 9006.3 | 0.9 | n/a | 20084.7 | 6.2 | n/a | 9041.4 | 1.0 | n/a | 117.1 | 0.0 |
| Foraminifera | n/a | 1.7 | n/a | n/a | n/a | n/a | n/a | 17.2 | n/a | n/a | n/a | n/a |
| Copepods nauplii | n/a | 15031.1 | 1.5 | n/a | 5214.2 | 1.6 | n/a | 7803.5 | 0.8 | n/a | 4040.8 | 1.7 |
| Polycheate larvae | n/a | 6028.7 | 0.6 | n/a | n/a | n/a | n/a | 4.6 | n/a | n/a | n/a | n/a |
| Tintinids | n/a | 2085.9 | 0.2 | n/a | 3429.7 | 1.1 | n/a | 16326.4 | 1.7 | n/a | 7493.1 | 3.1 |
| Shrimp larvae | n/a | 4493.6 | 0.5 | n/a | 765.7 | 0.2 | n/a | 4.4 | n/a | n/a | 328.8 | 0.1 |
| Arrow worms | n/a | n/a | n/a | n/a | 19658.9 | 6.1 | n/a | 690.4 | 0.1 | n/a | n/a | n/a |
| Insects | n/a | 4575.5 | 0.5 | n/a | 670.4 | 0.2 | n/a | 20.9 | n/a | n/a | 19026 | 8 |
| Fish eggs | n/a | 9734.7 | 1 | n/a | 278.6 | 0.1 | n/a | 611.7 | 0.1 | n/a | 873.9 | 0.4 |
| Amphipods | n/a | 6553.5 | 0.7 | n/a | n/a | n/a | n/a | n/a | n/a | n/a | n/a | n/a |
| Ostracods | n/a | n/a | n/a | n/a | 1155.2 | 0.4 | n/a | n/a | n/a | n/a | 6.3 | <0.00 |
| Crabs larvae | n/a | n/a | n/a | n/a | 526.4 | 0.2 | n/a | 57.7 | 0.0 | n/a | 73.4 | 0.0 |

Note: IRI = index of relative importance, n/a = no data, %v = %volume



*Significant difference between Northeast monsoon and Southwest monsoon from ANOVA (p<0.05)

Figure 2. Prey composition in the Pranburi River Estuary and Sirinaj Rajini Mangrove Ecosystem Learning Center during the Northeast and Southwest monsoon seasons.

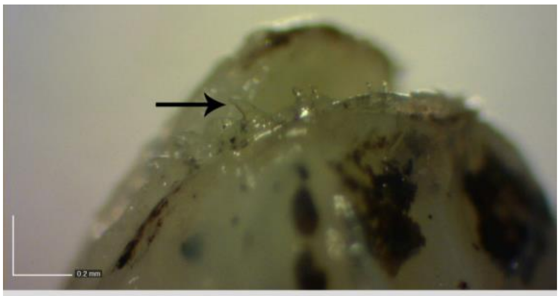


Figure 3. Premaxilla teeth with canine-like form of *Nestethus lankesteri*. Arrow indicates the canine-like teeth.

(Mok & Munro, 1991) and *Scatophagus argus* (Wongchinawit, 2007). The short gill rakers indicated the probability that this fish can feed on small prey items such as copepods, similar to what was found in *N. bicornis* (Mok & Munro, 1991). Several teleosts have a unique pharyngeal teeth form/shape that has been related to their feeding guild. For example, the durophagus fish have heavier round and strong pharyngeal tooth plates that exhibit large robust molariform teeth; *Anisotremus surinamensis* exhibits short densely packed conical teeth (Grubich, 2003). The non-durophagus fish tend to possess conical sharped form pharyngeal toothplates (Grubich, 2003). The pharyngeal teeth of *N. lankesteri* are numerous and canine-like in shape. The small teeth are arranged in a large number of parallel rows. This arrangement is similar to some fishes with well-developed pharyngeal teeth, which suggested that they are carnivorous (Mok & Munro, 1991). The pharyngeal teeth are believed to act as a grinding mill (Tibbetts & Carseldine, 2005). The appearance of pharyngeal teeth in *N. lankesteri* suggested that they may function in mastication of prey rather than being moved directly into the intestinal tract.

The intestines of *N. lankesteri* can be morphologically divided into three regions: the anterior intestine, middle intestine and posterior intestine under stereomicroscopic level (Figures 4A-4B). The morphology of the anterior intestines included the intestine bulb, similar to a previous report (Mok & Munro, 1991). The middle intestine was spiral shaped (Figure 4B) before entering into the posterior region. The characteristics of the posterior intestine were similar to the anterior intestine but somewhat smaller than that region. This was similarly noted in a previous observation (TeWinkel, 1939). The intestine coefficient of *N. lankesteri* in this study was 0.55, a measure that is used to categorize species into different trophic levels or feeding types. According to previous observations, a low IC values suggests more carnivorous feeding, 0.5-0.6 in *Sparus aurata* (Cataldi, Cataudella, Monaco, Rossi & Tancioni, 1987) and 0.8 in *Glyptosternum maculatum* (Xiong *et al.*, 2011), intermediate IC values suggest omnivorous feeding guild (2.0

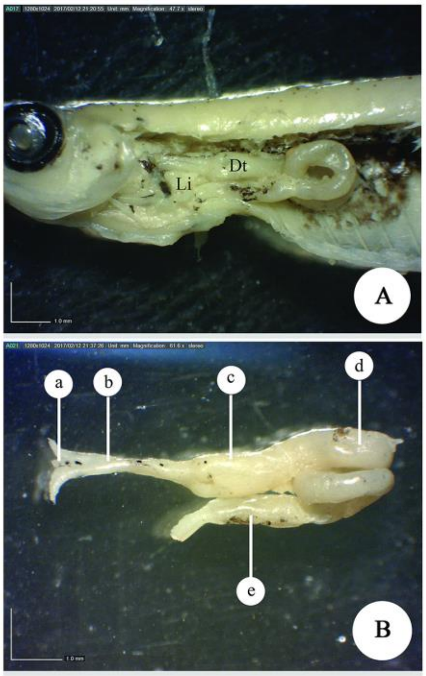


Figure 4. External morphology of the digestive tract of *Neostethus lankesteri*: (A) digestive tract orientation in the body cavity and (B) composition of digestive tract; a = pharyngeal tooth plate, b = esophagus, c = anterior intestine, d = middle intestine, and e = posterior intestine

*Ctenopharyngodon idellus*, Nie & Hong, 1963) and high IC values (above 3.0 in *Puntius stoliczkanus* (Senarat, Yenchum & Poolprasert, 2013)) suggest more herbivory. Therefore, the IC value of *N. lankesteri* is typically considered as carnivorous feeding.

## 3.3 Digestive tract structure

### 3.3.1 Oral cavity and pharynx

The oral cavity and pharynx were histologically observed, with each containing two layers including the mucosa and submucosa; however, the muscularis was not observed (Figures 5A-5B). The mucosa was lined with several layers of stratified polygonal epithelium cells (Figure 5B). Moreover, the large taste buds and mucous-secreting cells were located among the epithelial cells (Figure 5B). The tongue was central within the mandible, which showed a mucosal thickening without muscular fibers. No teeth were observed on the tongue, a feature that is no different from other teleosts (Abbate, Guerrera, Montalbano, Ciriaco & Germanà, 2012; Sadeghinezhad, Rahmati-holasoo, Fayyaz & Zargar, 2015). Note that the tongue was supported by large hyaline cartilage tissue (Figure 5C). The tongue plays a key roles in the ultimate acceptance or rejection of potential food items (Kruse & Stone, 1984).

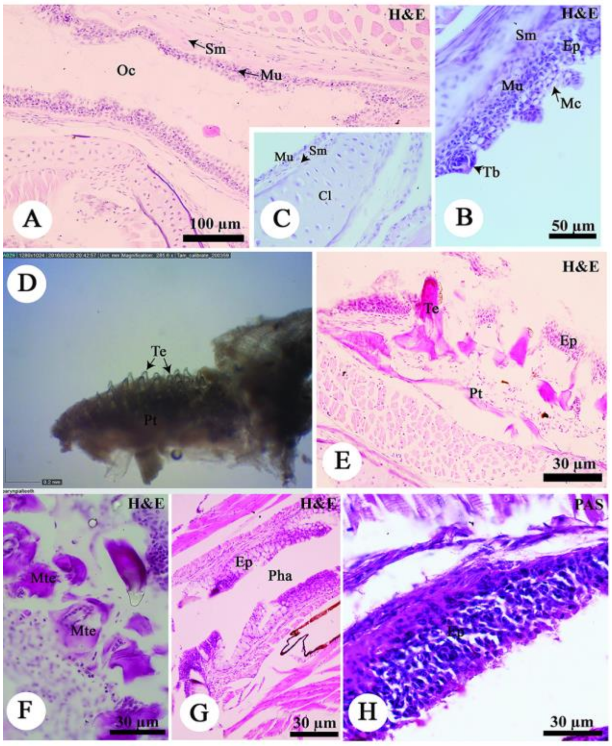


Figure 5. Oral cavity and pharynx histology of *Neostethus lankesteri*: (A-C) light micrograph of the oral cavity showing two layers of mucosa and submucosa, and (D-H) micrograph and transverse section of the pharyngeal toothplates. Abbreviations: Cl = cartilage tissue, Ep, epithelium, Mc = mucous-secreting cell, Mu = mucosa, Mte = mature teeth, Oc = oral cavity, Pha = pharynx, Pt = pharyngeal toothplate, Sm = submucosa, Tb = test bud, Te = teeth

Pharyngeal teeth were clearly observed in the pharynx (Figure 5D) and the pharynx was lined by canine-liked shaped teeth (Figure 5E). Histologically, the pharyngeal teeth consisted of elongated immature and mature teeth within the stratified epithelium (Figures 5E-5F). The taste buds and the mucous cells were also abundant and scattered among the epithelial cells (Figures 5G-5H).

### 3.3.2 Esophagus

The esophagus was observed throughout from the pharynx (Figures 6A-6B). The esophageal wall histologically consisted of four layers including the mucosa, submucosa, muscularis and serosa, respectively (Figure 6C). The longitudinal fold of the mucosal layer was lined by a protective simple cuboidal epithelium. Several mucous cells among the epithelial cells contained empty vacuoles and they were negatively stained with the H&E method (Figure 6D), but they positively reacted with the PAS method, indicating the presence of glycoproteins (Figure 6E). It is assumed that these glycoproteins are involved in transferring food to the intestine, which is also called the esophageal and intestinal junction (Harder, 1975; Cataldi *et al.*, 1987). A few layers of the lamina propria layer containing loose connective tissue and submucosa were not easily identified (Figure 6D).

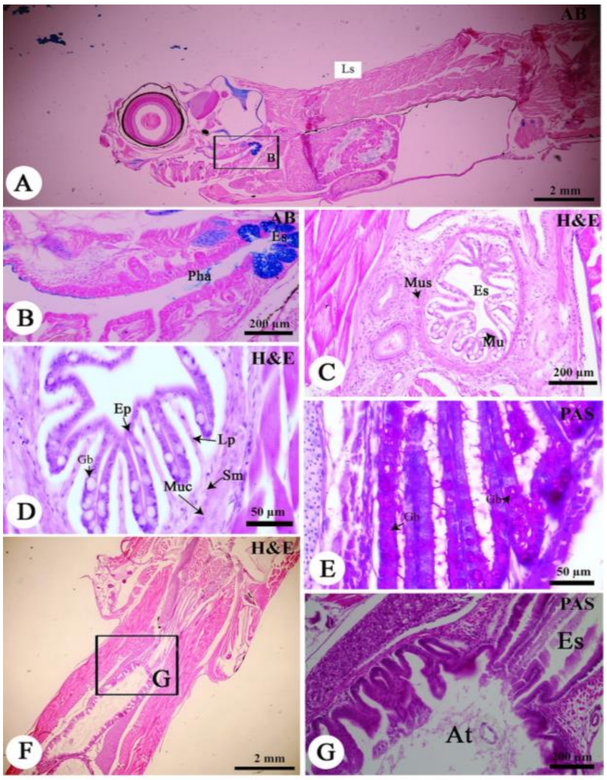


Figure 6. Light photomicrographs of the esophagus region in *Neostethus lankesteri*: (A-B) conjunction between pharynx and esophagus, (C-E) histological feature of esophagus showing several mucous cells in epithelial layer, and (F-G) the junction between the esophagus and intestinal region termed the esophageal and intestinal junction. Abbreviations: At, anterior intestine, Es = esophagus, Gb = mucous cell, Lp = laminar propria, Ls = lateral side, Mus = muscularis

### 3.3.3 Intestine

High magnification showed the junction between the esophagus and intestine (Figures 6F-6G). The esophageal lining changed from simple high cuboidal epithelium into simple columnar epithelium (Table 2). In the anterior intestine, the prominent longitudinal fold in the mucosal layer was very apparent (Figure 7A). The epithelial layer was covered by a simple columnar epithelium, while the muscularis mucosae and submucosa were difficult to identify conclusively. The middle and posterior intestines were commonly similar to the anterior intestines (Figures 7B-7C). However, there were significant differences (P<0.0001) in the longitudinal fold among the anterior (79.06±15.3 µm), middle (130.85±28.8 µm), and posterior intestine (43.09±18.6 µm). The goblet cells in the last portion of the intestine suggested an increased role in mucous production to lubricate food items, defecation, and also for protecting the epithelial layer rather than function in absorptive ability (Murray, Wright & Goff, 1994; Purushothaman *et al.*, 2016).

This study provided ecological and histological evaluations of the gut contents and morpho-histological characteristics of the digestive system in the priapium fish *N. lankesteri*. *N. lankesteri* is a carnivore and generalist feeder on zooplankton. This information provides knowledge of this fish on how it utilizes the PRE and SRMELC as a feeding ground.

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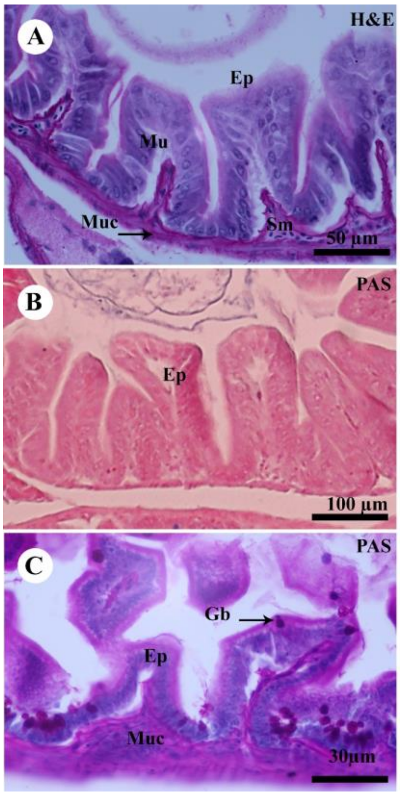

Figure 7. Transverse sections of intestinal regions of *Neostethus lankesteri* showing longitudinal folds and length differences among the three regions: (A) anterior intestine, (B) middle intestine, and (C) posterior intestine. Abbreviation: Gb = goblet cell (arrow)

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Table 2. Major histologically variation among pharynx, esophagus and intestine of *Neostethus lankesteri*

| Organs | Epithelial mucosa | Mucous cell | Submucosa | Muscularis (inner circular and outer longitudinal sub-layers) |
|---|---|---|---|---|
| Pharynx | SPE |  | present |  |
| Esophagus | SCE | present | present | present |
| Anterior intestine | SCE | present | present | present |
| Middle intestine | SCE | present | present | present |
| Posterior intestine | SCE | present | present | present |

Note: SCE; simple columna epithelium, SPE; stratified polygonal epitheliums and SSE; simple squamous epithelium

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