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CONE SNAIL RADULA: A REV IEW OF THE MORPHOLOGY AND STRUCTURAL PREVALENCE IN DIFFERENT FEEDING GROUPS

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Abstract

Cone snails utilize a hollow radular tooth to inject their target prey. The modification of this apparatus allows the predatory and venomous species to defend and hunt. The cone snail diet can be characterized into three feeding groups: piscivorous, molluscivorous, and vermivorous. A PRISMA-compliant systematic review was performed to compare similarities and differences of the radula from each feeding group. Studies comparing the radular morphological structures of five piscivorous *Conus* species, five molluscivorous, and three vermivorous *Conus* species eligible for inclusion were listed on ResearchGate and Google Scholar (September 2021). Seven (7) studies were screened for inclusion. The analysis of piscivorous radula to have two general types were consistently reported among included studies. Moreover, reports also conclusively stated the ontogenic changes in *C. magus'* radula, its highly analogous description to *C. catus*, and the elongated and simpler radula beneficial for the feeding strategy of *C. geographus* and *C. tulipa*. A high degree of similarity in terms of narrowness and simplicity of molluscivorous to piscivorous radula was also a common finding among studies. The extreme absolute length of *C. textile*; was similar to that of *C. geographus*, which employs a similar feeding strategy, and the shaft width percentage of *C. marmoreus* resembles that of *C. catus*. Studies also consistently emphasized the heightened interspecific variation observed in vermivorous radula. Despite the absence of description in some chosen *Conus* species, the information in this review provided consistency and implied a high correlation of feeding strategy to radular morphology.

Index Terms: *Conus,* PRISMA, Interspecific Variation, Molluscivorous, Piscivorous, Radula, Vermivorous

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1. INTRODUCTION

The radula of marine cone snails is primarily used to inject lethal venom into caught prey [1]. Various capture methods and feeding strategies allow them to use this hollow device most [2]. These predatory and venomous animals use hydraulics to propel a harpoon-like radula made up of a complex combination of conotoxins through the proboscis, paralyzing prey [3].

Prey selection specificity comprises the prey's type, size, and position targeted for envenomation [4]. Because of the significant interspecific competition among *Conus*, multiple feeding strategies and venom peptide sequence diversification have [5], [6], [7], [8], [9]. This genus of poisonous neo-gastropods has evolved one of the most advanced envenomation strategies known, allowing them to capture and feed on worms (vermivorous), mollusks (molluscivorous), and even fish (piscivorous) [10].

The most extensive studies included in this review were journal papers by [11] in 1999 and [12] in 1980. Despite the enormous data obtained via historical research and careful microscopic observation, these sources are outdated. Their references date back to Troschel in 1866 when he produced a dichotomous key for only 11 *Conus* species. According to the authors, these articles have previously shed light on the relationship between adapted radular analyses and their related eating groups and feeding strategies. However, areas still need to be highlighted to track the accuracy and certainty of the presented description. Therefore, this review will narratively synthesize obtained data from included papers to provide a greater understanding and perspective on the description of *Conus* radula. Further research on the radula of the chosen *Conus* species is necessary to understand their similarities and differences. This would outline what to expect when recognizing a *Conus* species' feeding mechanism and hunting strategy. In addition, understanding the distinctions in radula exhibited by the feeding group can reveal information about the species' specific ways of survival and evolutionary origin. Finally, researchers can study or uncover other unstudied cone snails once the evaluation produces consistent results.

2. METHODOLOGY

2.1 Formulation of Review Questions

The Preferred Reporting Items for Systematic Reviews and Meta-analysis criteria were followed for this systematic review. The following are the linked questions addressing the morphological similarities of *Conus* radula, which were formulated utilizing the patient population, intervention, comparison, and outcomes (PICOs) framework to outline the objectives:

1. What are the general characteristics of the radula of vermivorous, molluscivorous, and piscivorous *Conus* species?
2. What radular morphological structure is exclusive to vermivorous, molluscivorous, and piscivorous *Conus*?

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3. What structure of the radula of a selected *Conus* species can be morphologically distinguished from other species exhibiting a different feeding behavior?

2.2 Inclusion and Exclusion Criteria

Original articles comparing the radular morphology of the vermivorous species *C. capitaneus, C. imperialis,* and *C. terebra*; the molluscivorous species *C. bandanus, C. marmoreus, C. textile, C. aulicus,* and *C. gloriamaris*; and piscivorous species *C. catus, C. geographus, C. tulipa, C. bullatus, C. magus* were eligible. Endpoints were also qualified to distinguish the radula structures and features of piscivorous, molluscivorous, and vermivorous species. Studies that classified *Conus* species based on radula type were also included. Non-English articles, studies that did not analyze the radula morphology of selected species, and studies that did not compare radula characteristics were not eligible and were excluded. Several studies investigated the radula anatomy of *Conus* species with comparable eating behavior. Studies that only analyzed and compared the morphology of the selected *Conus* species without accounting for the radula were also excluded.

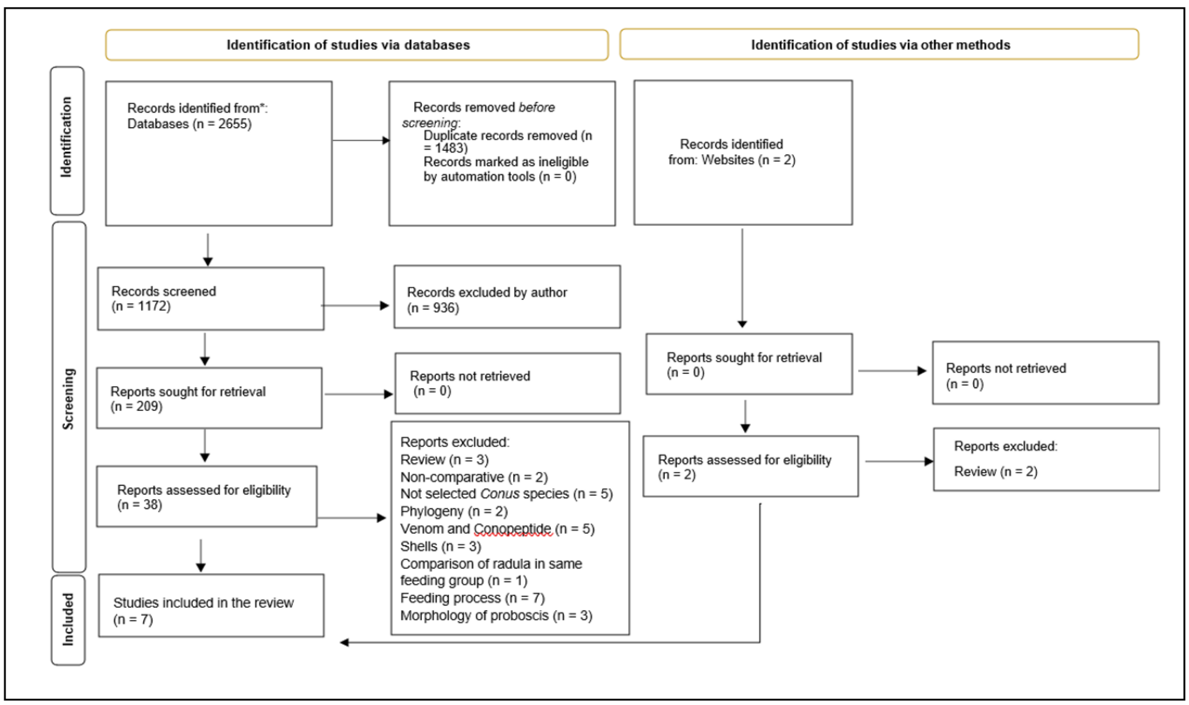

Figure 1: PRISMA Flowchart. *Research Gate and Google Scholar

2.3 Literature Search Method

From inception to 14 September 2021, a systematic search was conducted on the electronic databases ResearchGate and Google Scholar for research articles investigating the comparative radular morphology of selected vermivorous, molluscivorous, and piscivorous, *Conus* species using the following key search terms: "*Conus* radula morphology," "vermivorous *Conus* radula," "*Conus capitaneus* radula," "*Conus imperialis* radula," "*Conus terebra* radula.", "molluscivorous *Conus* radula,"

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"*Conus marmoreus* radula," "*Conus bandanus* radula," "*Conus textile* radula," "*Conus gloriamaris* radula," "*Conus aulicus* radula," "piscivorous *Conus* radula," "*Conus catus* radula," "*Conus geographus* radula," "*Conus tulipa* radula," "*Conus bullatus* radula," "*Conus magus* radula," The reference list of included articles was further scanned for potentially relevant studies. The publications obtained were classified as randomized or non-randomized studies.

2.4 Study Selection and Data Management

The review author evaluated search results for design and relevance independently and double-checked the titles and abstracts for accuracy. The reviewer got full versions of the articles that met the inclusion requirements. The review author then evaluated the studies obtained to establish the final selection of research included in the review. In addition, the review author extracted the data, which was then double-checked by another reviewer who had not participated in the extraction procedure. The reviewer retrieved bibliometric indices (authorship, year conducted, country of study), population characteristics (number, age/weight, species used, feeding method), intervention, and results from the included studies.

2.5 Data items

This systematic study aimed to collect and compare the various morphological structures of the selected *Conus* species. The following were the questions related to PICOs items:

1. *Participant Population*: Studies were considered for inclusion if the radula morphology of the selected piscivorous species *C. catus, C. geographus, C. tulipa, C. bullatus, C. magus* is compared to molluscivorous species *C. bandanus, C. marmoreus, C. textile, C. aulicus,* and *C. gloriamaris* and the vermivorous species *C. capitaneus, C. imperialis,* and *C. terebra*. Studies that compare the radula characters of the selected *Conus* species that exhibit different feeding behaviors were eligible.
2. *Intervention*: Studies were considered for inclusion if the radula morphology of the selected cone snail species has been observed through any microscope and compared with other selected *Conus* species.
3. *Comparison*: Studies were considered for inclusion if the comparison of radula morphology is observed through any microscope or other comparator interventions.
4. *Outcome*: The study outcome did not form part of the selection process. The results were structured into primary and secondary outcomes.

Primary Outcomes

1. Comparison of radula morphology based on diet and feeding behavior.
2. The morphologically distinguished radula structure of individual selected *Conus* species.

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Secondary Outcomes

1. Relationship of radula morphology to feeding behavior.
2. The similarity of radula structures.

2.6 Risk of Bias Assessment for Individual Studies

For non-randomized studies, the researchers utilized the Cochrane Collaboration's risk assessment tool and the JBI Critical Appraisal Checklist for Quasi-Experimental Research. This research study included randomized and non-randomized studies on the selected *Conus* species. The JBI Critical Appraisal Checklist for Quasi-Experimental Studies will be used to evaluate the methodological quality of studies that do not utilize randomization to assign individuals; the instrument will be used to address the likelihood of bias in the design, conduct, and analysis. On the other hand, the Cochrane Collaboration's risk assessment tool will assist researchers in assessing the bias of randomized studies, correcting design faults, conducting analysis, and reporting publications included in the systematic review.

3. RESULTS

Following the application of the inclusion and exclusion criteria, seven (7) publications remained, all of which are non-randomized studies. Table 1 shows the samples and species used in original research articles, the radula structures studied, species compared, and outcome measures.

3.1 Included Studies

The seven (7) publications included in this systematic review evaluated the radular tooth morphology of three (3) feeding behaviors of selected *Conus* species, making them eligible for inclusion (summarized in Table 2). Studies were conducted in the United States [11], [12], [13] and France [14], [15], Spain [16], and India [17]. James (1980) [12] compared C. *catus, C. tulipa, C. magus,* and *C. textile* radular teeth characteristics; Kohn *et al*., [11] compared the radular teeth morphology of *C. marmoreus* and *C. catus*; Le Gall *et al*. [14] compared the radular teeth morphology of *C. textile*, and *C. catus*; Franklin *et al*. [17] compared the radular teeth morphology of *C. terebra* and *C. textile*; Tenorio [16] compared the radular teeth morphology of *C. textile*, and *C. imperialis*; Dutertre and their team [15] compared the radular teeth morphology of C*. textile, C. marmoreus, C. imperialis*, and *C. geographus*; and Nyabakken [13] compared the radular teeth morphology of *C. capitaneus, C. imperialis, C. catus, C. geographus, C. magus, C. tulipa, C. gloriamaris, C. marmoreus*, and *C. textile.*

3.2 Excluded Studies

Three (3) review studies, two (2) non-comparative, five (5) studies that used different *Conus* species, two (2) phylogeny studies, five (5) venom, and conopeptide studies, three (3) on shell morphology, one (1) on comparison of radula with the same feeding type, seven (7) on the feeding process, and three (3) on proboscis morphology were excluded.

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3.3 Primary Outcomes: Radula Character Analysis

Three (3) studies [11], [12], [13] consistently indicated the presence of two barbs, an elongated shaft, and the absence of a spur as collective characteristics of the piscivorous species radula. However, all three (3) studies suggest that a slight variance might be recognized as having a third posteriorly large barb that curves at the end among other species that adopt comparable feeding behavior. In addition, all included studies identified molluscivorous radula as having an elongated radular tooth with one barb and one blade at the anterior end, a serrated shaft that usually terminates into a cusp, a waist visible in some species but not in others, and a lack of a basal spur.

Furthermore, according to two studies [11], [12], the radula tooth of vermivores exhibits significant interspecific variation but is commonly distinguished by the presence of one or two barbs at the tip, one of which can be replaced by a blade [17] or contain four barbs [13]. However, included studies consistently observed a spur at the posterior end of the vermivorous radula.

3.3.1 Comparison 1: Piscivorous Radula Compared with Molluscivorous Radula

All of [12], [13], [17], and their colleagues found a typically similar radula in piscivorous and molluscivorous species, with fewer interspecific differences in piscivorous radula than in other diet groups. Similarly, [16] observed an absence of a basal spur and serrations and a terminal cusp modified into an accessory process in piscivorous and molluscivorous radula teeth of the subfamily Coninae. When comparing molluscivorous and piscivorous species' radular teeth, the latter can be identified by having two types of radular teeth [11], [12], [13].

Similarly, [15] associated the comparison of piscivorous to molluscivorous group radula to venom duct features, with piscivorous species having a comparatively small duct (two to three times the length of the shell) and vermivorous and molluscivorous species having a lengthy duct (up to six times the length of the shell). This organ's size varies with the size of the radula and piscivorous and molluscivorous cones generally have a large and well-developed radular sac. On the other hand, some piscivorous animals, including the lethal C. geographus, have a more straightforward, long, slender radula that lacks the long accessory process. Its net-hunting technique is similar to molluscivorous species such as *C. textile,* having similar radular properties.

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Table 1: Summary Samples and Species Used In Original Research Articles, the Radula Structures Studied, Species Compared, And Outcome Measures

<table>
<tr><th rowspan="2">First author, year (Country of origin)</th><th rowspan="2">Number of samples (Age/weight)</th><th rowspan="2">Selected species used</th><th rowspan="2">Feeding behavior</th><th rowspan="2">Study Design</th><th rowspan="2">Intervention (Radula structures compared)</th><th rowspan="2">Comparison</th><th rowspan="2">Outcomes (measures)</th><th colspan="5">Results</th></tr>
<tr><th>C. catus</th><th>C. magus</th><th>C. tulipa</th><th colspan="2">C. textile</th></tr>
<tr><td>James, 1980 (U.S.A)</td><td>22</td><td>C. catus,
C. tulipa,
C. magus,
C. textile</td><td>P
P
P
M</td><td>Non-randomized Study</td><td>SEM Observation (Tooth, Basal spur, Barbs)</td><td>Molluscivorous VS Piscivorous Radula</td><td>Tooth length
Shell: Tooth ratio
Basal spur
Barbs</td><td>2.5mm
16.0
No
3</td><td>2.9mm
15.5
No
3</td><td>4.4mm
15.5
No
2</td><td colspan="2">14.2mm
3.5
No
2</td></tr>
<tr><td>Kohn, 1999 (U.S.A)</td><td>Primitive species, Species from functional feeding group, 118 Indo-Pacific Conus species</td><td>C. marmoreus
C. catus</td><td>M
P</td><td>Non-randomized Study</td><td>SEM Observation (Present and Absent characters)</td><td>Molluscivorous VS Piscivorous Radula</td><td>Barb 1 – Barb 5
Blade
Serration
Cusp
Waist
Spur</td><td colspan="3">C. marmoreus
Barb1
Present
Present
Present
Absent
Absent</td><td colspan="2">C. catus
Barb 1, 2, 3
Absent
Absent
Absent
Absent
Absent</td></tr>
<tr><td>Le Gall, 1998 (France)</td><td>3 Conus species</td><td>C. textile
C. catus</td><td>M
P</td><td>Non-randomized Study</td><td>SEM Observation (Tooth length and tip)</td><td>Molluscivorous VS Piscivorous Radula</td><td>Tooth length
Tip</td><td colspan="3">C. textile
Long harpoon posteriorly directed with a curved tip
Barb on one side and a barbed blade on the other side</td><td colspan="2">C. catus
Long harpoon not present
Large blade on one side with a curved tip on the other side.</td></tr>
<tr><td rowspan="2">Franklin, 2007 (India)</td><td rowspan="2">22 Conus species from Indian coastal waters</td><td rowspan="2">C. textile
C. terebra</td><td rowspan="2">V
M</td><td rowspan="2">Non-randomized study</td><td rowspan="2">SEM observation (Absent and present characteristics)</td><td rowspan="2">Molluscivorous VS Vermivorous Radula</td><td>Scanning Electron Microscopy
C. terebra</td><td>Barb number
2</td><td>Blade
Absent</td><td>Basal Spur
Present</td><td>Serration
Present</td><td>Waist
Present</td></tr>
<tr><td>C. textile</td><td>2</td><td>Absent</td><td>Absent</td><td>Present</td><td>Present</td></tr>
<tr><td rowspan="2">Tenorio, 2011 (Spain)</td><td rowspan="2">Primitive species from family Conidae and family Conilithidae</td><td rowspan="2">C. textile
C. imperialis</td><td rowspan="2">M
V</td><td rowspan="2">Non-randomized study</td><td rowspan="2">SEM observation (radular teeth size; Absent and present characteristics)</td><td rowspan="2">Molluscivorous VS Vermivorous Radula</td><td>Radula Anatomy
C. textile</td><td colspan="5">Description
The radular tooth in Cylinder species has the anterior section of the tooth greatly elongated compared to the posterior section of the tooth; a short barb and blade are present; a terminating cusp is present; a basal spur is absent; the waist is not noticeable.</td></tr>
<tr><td>C. imperialis</td><td colspan="5">The anterior section of the radular tooth is shorter than the posterior section; basal spur is present; the blade extends nearly the entire length of the anterior section of the tooth; the terminating cusp is exposed.</td></tr>
<tr><td>Dutertre, 2016 (France)</td><td>Six Conus species</td><td>C. geographus
C. textile
C. imperialis
C. marmoreus</td><td>P
M
V
M</td><td>Non-randomized study</td><td>Scanning electron and confocal microscopy (Length and width of teeth)</td><td>Molluscivorous VS Vermivorous VS Piscivorous Radula</td><td>Radula sac and teeth</td><td colspan="5">Description
The radula of piscivorous species has a long shaft and the tip containing a blade, a barb, and a long accessory process that is hooked at the distal end like a mini harpoon. C. geographus use a simpler radula devoid of the long accessory process. Finally, the worm hunters such as C. imperialis produce a short, thick radula.</td></tr>
<tr><td rowspan="5">Nybakken, 1990 (USA)</td><td rowspan="5">89 species (Adult and juvenile)</td><td rowspan="5">C. capitaneus
C. catus
C. geographus
C. gloriamaris
C. imperialis
C. magus
C. marmoreus
C. textile
C. tulipa</td><td rowspan="5">V
P
P
M
V
P
M
M
P</td><td rowspan="5">Non-randomized study</td><td rowspan="5">SEM observation (radular teeth size; Absent and present characteristics)</td><td rowspan="5">Molluscivorous VS Vermivorous VS Piscivorous Radula</td><td colspan="6">Morphological Classification of Conus Radula</td></tr>
<tr><td>Type 1</td><td colspan="5">C. chaldeus, C. miles, C. abreviatus, C. aponsalis, C. rattus, C. triatus, C. litteratus, C. leopardus, C. arenatus, C. taeniatus, C. ceylanensis, C. scabriusculus, C. capitaneus, C. vexillum, C. balteatus, C. nux, C. milliaris, C. coronatus, C. gladiator, C. regularis, C. pularius, C. vexillum.</td></tr>
<tr><td>Type 1b</td><td colspan="5">C. dali, C. textile, C. pennanceus, C. marmoreus, C. episcopus</td></tr>
<tr><td>Type 2</td><td colspan="5">C. catus, C. striatus, C. purpurascens, C. magus</td></tr>
<tr><td>Type 3</td><td colspan="5">C. brunneus, C. zonatus, C. imperialis</td></tr>
</table>

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Table 2: Risk of Bias of Non-Randomized Included Studies

	James (1980)	Nyabakken *et al.* (1990)	Kohn *et al.* (1999)	Le Gall *et al.* (1999)	Tenorio (2011)	Franklin *et al.* (2015)	Dutertre *et al.*, (2016)
1. Clear and cause-effect	YES	YES	YES	YES	YES	YES	UNCLEAR
2. Similar comparisons	YES	YES	YES	YES	YES	YES	YES
3. Similar treatment other than the intervention	YES	YES	YES	YES	YES	YES	N/A
4. Control group	NO	NO	NO	NO	NO	NO	UNCLEAR
5. Multiple measurements	YES	YES	YES	YES	YES	YES	NO
6. Follow-up description	YES	YES	YES	YES	YES	YES	YES
7. The exact outcome measurement	YES	YES	YES	YES	YES	YES	YES
8. Reliability of outcome measurements	YES	YES	YES	YES	YES	YES	YES
9. Appropriate statistical analysis	YES	YES	YES	YES	YES	YES	YES
Total (%) and quality rating*	8/9 (88%) Good	8/9 (88%) Good	8/9 88% Good	8/9 (88%) Good	8/9 (88%) Good	8/9 (88%) Good	5/9 (55%) Moderate

3.3.2 Comparison 2: Piscivorous Radula Compared with Vermivorous Radula

Piscivorous radula can be divided into two types: those with a long radula with an anteriorly serrated shaft, a slightly enlarged base, two barbs that lack an evident waist, blade, and spur as observed in *C. geographus* and *C. tulipa*, and those with teeth that are slightly shorter and lack serration and a waist, but still have a slightly enlarged base and a basal spur as observed in *C. catus* and *C. magus* [13], [15]. The highly diversified vermivorous radula, on the other hand, revealed a morphologically distinct shorter anterior part with four barbs at the tip, one of which contains serrations, and a waist observed posteriorly to the barbs that culminate into a conspicuous basal spur, as seen in *C. terebra* [17]. [11] and [12] observed that the presence-absence of a spur is a significant and valid discriminant since the spur is not present in the extended radula of piscivores and molluscivores but is commonly found on the thick and short teeth of vermivores.

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3.3.3 Comparison 3: Molluscivorous Radula Compared with Vermivorous Radula

According to [15], molluscivorous species have a large and well-developed radular sac, whereas worm hunters such as *C. imperialis* have a short and thick radula. Moreover, [16] revealed that the anterior section of *C. imperialis* tooth is shorter than the posterior end, which is spur-bearing *C. gloriamaris*, *C. marmoreus*, and *C. textile* all displayed a typical radular morphology of a molluscivore *Conus* in which the anterior portion is highly elongated and is usually several times longer than the posterior region. The serration may be external or completely internal. The anterior tip has two unequal-sized barbs, the smaller of which is inflated laterally and lacks a blade and spur. Vermivorous *C. imperialis*, on the other hand, is recognized by four barbs near the shortened anterior end, one of which makes a noticeable angle with the shaft, which bears short serration. The most noticeable barb is the longest, with a broad blade, and all of the barbs are recurved or hooked; there is a slight waist posterior to the barbs. The shaft extends to its maximum diameter posterior to the waist and ends in a large base with a large spur lacking a cusp [13].

According to [11], *C. marmoreus* is identical to *C. bandanus*, except that the former has just one barb with a tooth that lacks a defined waist, and the maximum base width is about double the shaft width. This differs from the vermivorous species *C. terebra*, which has two barbs at the front end of the tooth shaft, as described by [17]. The serration terminates with an enlarged terminal knob at a large cusp distal to the tooth shaft anterior to the waist. Compared to other vermivorous species with prominent spurs, such as *C. capitaneus*, it has a less developed short spur. According to [13], a prominent but small spur in which the tooth has approximately equal anterior and posterior sections, and the anterior half is terminated by a single barb and a blade extending posteriorly to the end of the waist. The serration usually ends in a prominent cusp; both the cusp and the serration are internal. The tooth's posterior half is slightly larger in diameter and has a slightly expanded rounded base.

3.3.4 Morphologically Distinguished Structures

The radula of *C. catus* represents the most typical tooth observed in piscivorous *Conus*. On the other hand, the radula of this species has the largest tooth-to-shell ratio of any species, indicating the tooth's small absolute and relative size. Further, the anterior terminal knob of *C. magus* is significantly larger than other species, distinguishing its radula from other piscivorous cone snails [12]. In addition, *C. tulipa* and *C. geographus* have similar radulas, according to [12]; however, the tooth of *C. tulipa* can be identified by a long shaft with a slightly enlarged terminal knob, an anterior end with one blade on one side and a small barb on the other. None of the studies reported distinguished the *C. geographus* and *C. bullatus* radula structures.

According to [12], the *C. textile* radula's distinguishing structure is its great absolute length and low shell-to-to-tooth ratio. Additionally, [11] revealed that the tooth of *C. marmoreus* is the shortest among molluscivorous species. The morphologically distinct radula features of *C. aulicus*, *C. bandanus*, and *C. gloriamaris* were not recorded in any studies. Finally, [17] reported that the shell length to tooth length ratio of *C. terebra*

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differentiates the species' radula from those of other similarly related vermivorous *Conus*. [13] Characterized the *C. capitaneus* radula type from other vermivores by identifying it as having a tooth with equal anterior and posterior parts. The anterior half was terminated by a single barb and a blade that extends posteriorly more than halfway to the waist on the opposite side.

3.4 Secondary Outcomes

3.4.1 Relationship of Radula Morphology with Feeding Behavior

One (1) study differentiated between the prey capture mechanisms of molluscivorous and vermivorous feeding cone snails, as well as how the function of teeth in molluscivorous species differs from that of vermivores to envenomate a prey. The latter uses only one tooth in a single feeding session, whereas the former may use multiple teeth in a single feeding session [15]. Each tooth's base is detached from the proboscis and inserted like a hollow arrow into the prey's body. The victim's body is subsequently eaten once the proboscis is retracted and the rhynchodeum is stretched into the victim's shell opening.

Two (2) studies [11], [12] reported that vermivorous *Conus* species have more variations in their radular teeth than other feeding groups. Since there is little dietary overlap among vermivorous species, the diverse variety of morphologically distinct tooth forms is most likely due to trophic specialization [11]. According to [12], vermivorous species have distinct radular tooth morphology, as demonstrated in the diets of other species in the same group. *Conus* species that only feed on polychaetes have a distinctive radular tooth shape that distinguishes them from vermivores which feed on echiuroids and enteropneusts. While there is a significant variation in radular morphology in vermivorous *Conus*, species exhibiting this type of feeding behavior, as reported by [11], generally employ a similar mechanism to impale the prey, in which the venom is injected after the prey is successfully struck by the barbs at the apex of the radular tooth, as well as the proboscis' lip firmly holds the base of the tooth. As a result, the worm's proboscis shortens, dragging it into the widened rhynchodeum.

Five (5) studies examined the association between piscivorous species' radular anatomy and feeding style. According to [12] study, there are far fewer variations in the radular teeth of piscivorous species of *Conus*, such as *C. catus* and *C. magus*, compared to vermivore teeth, which may indicate that those who feed strictly on a variety of fish in the families of Blenniidae and Gobiidae have a well-adapted tooth structure. Additionally, according to [15], piscivorous species have a large and well-developed radular sac. Radial morphological diversity emerges to adapt to the prey-hunting strategy. For example, the net-hunting *C. geographus* has a long and slender radula that lacks a long accessory process, allowing it to swallow the prey before envenomation [11]. Furthermore, piscivorous species teeth with smaller and fewer barbs, such as those observed in *C. geographus* and *C. tulipa*, may deliver potent venom to a more susceptible region of the prey's body because they can penetrate deeper into the prey's body. Thus, according to [14], the radula tooth of *C. catus* does

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have a long harpoon with three barbs at the tip that is posteriorly directed to tether the fish and utilize the "hook-and-line" strategy to envenomate their prey.

Finally, [13] observed the ontogenic transition of magus radula from juvenile to adult. The species' radular development has demonstrated that juveniles eat worms and later transition to fish as adults. The post-metamorphic tooth is not thoroughly chitinized and is just utilized to absorb chitin-specific dyes. Furthermore, because juvenile radula appeared in both sexes, the observed ontogenic radular alteration is unrelated to sexual dimorphism.

3.4.2 Similarity of Radula Structure

Closely related species and those with similar diet habits could have nearly identical radula structures [15]. Serration length, presence of barbs, blades, cusp, and spur, the relative breadth of the tooth base, and the ratio of total radula length/shell length, are all essential secondary features. Piscivorous species like the *C. geographus* contain a simple radula devoid of a long accessory process resembling the radula teeth of molluscivorous species that are long and slender.

According to one (1) study [11], *C. catus, C. magus*, and *C. tulipa* have radular teeth similar to *C. geographus. In particular, C. catus and C. magus* were described as having typical piscivorous radular teeth. Meanwhile, *C. tulipa* and *C. geographus* radula are piscivores with venom capable of rapidly paralyzing their prey and are characterized by a long, anteriorly serrated shaft with a slightly larger terminal knob. The reduced armature in these two species indicates an adaptive significance for increased venom toxicity when injected for either predation- or defense-evoked predation or defense. Both were recorded to execute the net-hunting strategy [11]. Furthermore, according to [15], the evolution of piscivorous and molluscivorous diets may have originated to deploy defensive strategies against fish predators.

Reported by [11], the radula of the molluscivorous feeder *C. marmoreus* and the piscivorous feeder *C. catus* have morphological characteristics that are similarly exhibited by both species. The radula tooth lacks a blade, serration, cusp, and waist. Additionally, the radular teeth of molluscivorous *C. marmoreus* and *C. bandanus* are almost identical. Both teeth lack a definite waist, a maximum base width of about twice the shaft width, and about 10% of tooth length as measured from specimens mounted on slides.

The studies of [11] and [12] reported that the radula tooth of vermivorous feeders was highly diverse and showed significant interspecific variation. However, [11], [12], and [17] reported the presence of a basal spur from every observed vermivorous feeding *Conus*.

4. DISCUSSION

Data from seven (7) research were combined to provide a pooled overview of findings concerning the morphological differences in radula structures reported in cone snails with various feeding habits. Regarding the risk of bias, all studies were assessed as

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moderate to good. However, a meta-analysis is impossible due to the heterogeneity of the research, comparator, and outcome measures.

The review's results should be interpreted with the following considerations: the studies were assessed as moderate to good in risk of bias, and different tools and sample preservation methods were employed in viewing the radula of various cone snails. The appropriateness and similarity of comparators were not uniform among the included studies, and the diversity in outcome measuring precluded a meta-analysis.

4.1 Primary Outcomes: Radula Comparison Based on Diet and Feeding Behavior

The results consistently reported that piscivorous cone snails appear to have two distinct types of radulae. Four (4) of the included studies [11], [12], [13], [17] reported that piscivorous radula is generally large and elongated with three barbs and can be serrated or not, but all possess a narrow base that lacks spur. Seven (7) studies [11], [12], [13], [14], [15], [16], [17] consistently reported the radular morphology commonly observed in *Conus* species with a molluscivorous feeding behavior to have an elongated radular tooth that has one barb and one blade at the anterior end, with a serrated shaft that commonly terminates into a cusp, with a waist evident in some species, and a basal spur lacking in every species. Two (2) studies [11], [12] have shown that the radula of vermivorous *Conus* varies significantly, but it can have up to four barbs at the tip, according to Franklin *et al.*, 2007, which may or may not contain serration in some species, a waist visible in some species, and a basal spur at the posterior end of the radula present in all vermivorous species [11], [12], [13], [17].

Piscivorous and molluscivorous *Conus* radula has similar radula and exhibits less interspecific variation among species than the diverse vermivores. Molluscivorous *Conus* exhibit a single type of radula characterized by showing two anterior barbs and, in some species, possess a serration and waist, a terminal knob, and an absent spur as recorded in *C. textile* [12], [16], [17], *C. marmoreus* and *C. bandanus* [11]. Compared to two general radula types of piscivores that could either have three barbs at the tip and a prominent knob, as recorded in *C. catus* and *C. magus*, and the second type, as recorded in *C. tulipa* and *C. geographus* as having one barb and one blade at the tip, a long shaft with, a slightly enlarged terminal knob with evident serrations [12]. The base of piscivorous radula resembles those of molluscivores in being narrower and more straightforward than vermivores.

Further, [12], [13], and [17] concluded that the comparison of piscivorous and molluscivorous radula is often described to be generally similar in context due to their unique and consistent nature to the rather diverse terms of vermivorous radula. There is less interspecific variation in piscivorous radula than in other diet groups. [16] Supported this by referencing the general characteristics of the subfamily Conidae wherein the radular teeth of piscivorous and molluscivorous species often exhibit an absent basal spur, serrations, and a terminating cusp modified into an accessory process. However, compared to molluscivores, [12] stated that they only possess one type of radular teeth with two anterior barbs and, in some species, possess a serrated shaft or terminal knob.

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The base of piscivorous species generally resembles those of molluscivores in being narrower and simpler than vermivorous species, as observed in *C. catus* and *C. magus* [11]. The study of [11] has a good rating in the risk of bias assessment and compared radula based on present-absent characters. This study shows that some piscivorous species, such as the deadly *C. geographus*, use a simple, long, and slender radula devoid of the long accessory process for its net-hunting procedure and is said to be resembling those of the molluscivorous species such as *C. textile*; that also exhibit similar radular characteristics according to [15]. The results suggest that the radula of piscivores and molluscivores are generally identical, as observed in simple, long, and slender radula, with a narrow base that lacks a spur.

Results in this review paper consistently show that the radulae of piscivores are slender and elongated compared to the highly diverse short, thick, and spur-bearing radula of vermivores. The results presented by [15] should be interpreted with the context of the study having a moderate risk of bias with unclear cause and effect and control group. Two (2) studies [12], [17] consistently reported two general types of radulae observed in piscivores. Moreover, the results consistently showed that both radula types' of waist and spur are absent. Whereas vermivorous cone snails have highly diverse radulae but are distinguishable, commonly short, and thick with noticeable spur. *C. geographus* and *C. tulipa* have a radula that is exceptionally long, with a serrated shaft and a base that is slightly enlarged, and a tip with a small blade on one side and a barb on the other, without waist, blade, and spur which is morphologically different to another radula type observed in piscivorous *C. catus* and *C. magus* radula which have a shorter shaft that lacks serrations and waist, a slightly enlarged base, and a tip with two opposing barbs and a third outwardly protruding that is also lacking a basal spur.

Lastly, both radulae recorded in piscivores are morphologically different from the radula of vermivorous *C. imperialis* have a shorter anterior section with four barbs at the tip, with one of the barbs containing short serrations, an evident waist, and a massive base that includes a prominent spur. Which is also morphologically different from the radula of *C. capitaneus* with equal anterior and posterior section parts; the anterior end bears a single barb and a blade that extends posteriorly more than halfway to the waist on the opposite side, present serration, waist, and prominent cusp, with the posterior end slightly enlarged bearing a prominent basal spur similar to *C. imperialis*. A study by [13] was assessed to have a good risk of bias rating. It used an indirect surrogate way of reporting results of radular comparison based on grouping species based on radula types. *C. terebra* radula has a tip that bears two barbs, serration, cusp, waist, and a poorly developed short spur compared to a piscivorous radula with three barbs, serration, waist, cusp, and an absent spur. In comparison, the study by [17] has a good rating in the risk of bias and presented results based on scanning electron micrographs. Presently, the presence-absence of a spur is valuable and a valid discriminant since the spur is not present in the elongated radula of piscivores and molluscivores but is commonly found on the thick and short teeth of vermivores.

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4.2 Secondary Outcomes: Relationship of Radula Morphology with Feeding Behavior and Similarity of Radula Structure

Similar caution should be exercised in interpreting the intervention results for the secondary outcome. Reported by [11], *Conus* radula is an adaptation of cone snails to different prey-hunting strategies due to trophic specialization and varying prey availability. While according to a study by [12], radular morphology provides information that enables the estimation of the diet of certain *Conus* species. Thus, it suggests that the radular tooth is a species-specific character, and the type of radula a *Conus* possesses is related to the species' diets and feeding behavior.

Piscivores that hunt mobile prey require a radula to properly administer the venom and initiate immobilization as rapidly as possible; otherwise, the prey will escape. The general radular characteristic of piscivores includes narrow and simple radula bases with smaller and fewer barbs [11], [12]. Moreover, [13] study stated that this characteristic allows piscivorous radula to penetrate deeper into the prey and deliver the venom to the most vulnerable body region. Aside from general radula characteristics, piscivores have a unique radular characteristic that varies depending on their prey-capture strategy. Findings of [14] reported that piscivorous *Conus* species that utilized the "hook-and-line" technique have longer radula with posteriorly directed barbs that allow immobilization and the ability to tether the fish and secure the prey. [11] Stated that piscivores that utilize the net-engulfment strategy also have long and slender radula but do not possess long accessory processes to allow the engulfment of the prey before envenomation. In addition, [13] also reported that specific species have a transition in the diet as the radula matures, such as in *C. magus,* which demonstrated that the radular morphology of juveniles of this species is adapted for hunting worms, and in adulthood, the radula changes to adapt a fish-hunting diet.

Investigated by [15], the prey capture mechanisms of molluscivores and vermivores and the function of radular teeth. They observed that vermivores capture prey with a single tooth, while molluscivores capture prey with multiple teeth, with the base of the tooth detached from the proboscis and inserted into the prey's body. Furthermore, unlike vermivores, which drag their prey into their rostrum by dragging the thick base of their radula through the proboscis, molluscivores fire powerful, deep penetrating shots and easily detach their radula from their proboscis due to its thin base, leaving multiple radulae on their prey, quickly paralyzing the entire body.

In addition, vermivores, similar to piscivores, use a single radula to envenom their prey, as [11] reported. However, radulae characteristics of vermivorous *Conus* allow the species to firmly hold the base of the radula through the tip of their proboscis such that when they shorten their proboscis, their prey will be dragged into their rostrum to be engulfed [11]. In addition, [11] also mentioned that vermivorous species have highly diverse radular morphology; however, even with significant variation in radula, these species generally employ similar mechanisms in impaling and engulfing their prey.

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In terms of radula structure similarity, the radula of piscivorous species is often larger proportional to their body size than those of molluscivorous and vermivorous species. According to the findings, the radula of piscivorous *C. catus, C. magus*, and *C. tulipa* are identical to that of *C. geographus*. Furthermore, the radula characteristics of *C. tulipa* and *C. geographus* are similar, and their reduced armature implies adaptive importance, which promotes toxicity. These results suggest that the fish-hunter *Conus* species share radula features critical in prey acquisition. Furthermore, the radula architecture of molluscivorous *C. marmoreus* and *C. bandanus* are highly similar [11], and all vermivorous-eating *Conus* have a basal spur [12]. Lastly, the results suggest that the radula of the selected *Conus* species may have a nearly identical structure to species with the same feeding habit or closely related species.

5. CONCLUSION

Radular tooth characteristics of *Conus* species from the piscivorous, molluscivorous, and vermivorous feeding groups were compared and reported. Due to evolution, cone snails' adaptation to prey has resulted in changes to their radular teeth. The reviewed cone snails have traits that distinguish them from other feeding groups while maintaining different morphological structures. The classification of piscivorous radula into two broad kinds is consistent. Conclusive evidence supports *C. magus*' ontogenic alterations, its highly similar description to *C. catus*, and the elongated and simpler radula beneficial to *C. geographus* and *C. tulipa*'s feeding strategies. The remarkable resemblance between molluscivorous and piscivorous radula in narrowness and simplicity was likewise constant. It includes the extreme absolute length of *C. textile*, which is comparable to *C. geographus* and utilizes a similar feeding strategy, as well as the shaft width percentage of *C. marmoreus*, similar to *C. catus*. Moreover, the significant interspecific variation observed in vermivorous radula was emphasized. *C. capitaneus*, *C. imperialis*, and *C. terebra* radula have distinct traits and modified parts. Furthermore, although most studies gave consistent descriptions, several criteria or categorical analyses cited were obsolete and occasionally overlapped, with missing descriptions or unexpected appearances of observed sections. A more recent comparative investigation of radula morphology in a larger range of cone snails is highly recommended.

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