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Original Article

The tooth morphology of juvenile Pacific nurse sharks *Ginglymostoma unami* (Chondrichthyes: Ginglymostomatidae)

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Abstract
Nurse sharks (family Ginglymostomatidae) are a small group of sharks that currently consists of four different species. These species are distributed all over the globe, each occupying a specific geographical region. The last described nurse shark species, the Pacific nurse shark (*Ginglymostoma unami*), is found exclusively on the West coast of America from the Southwest of Baja California and the Gulf of California (Mexico) to Peru. This species was previously synonymized with the Atlantic nurse shark (*Ginglymostoma cirratum*), but described as separate in 2015. For this reason, some data on tooth morphology, especially that of juvenile individuals, is missing. This study examines a jaw of a juvenile Pacific nurse shark and shows the change in the tooth morphology of this species over the course of its life. In addition, this work compares the tooth morphology of the different nurse shark species and provides an overview of how they can be differentiated.

Keywords: Chondrichthyes; *Ginglymostoma* spp.; nurse sharks; Pacific Ocean; tooth morphology; shark jaws

1 | INTRODUCTION

While many shark species are popularly known for their dangerous appearance or aggressive feeding behavior, nurse sharks (family Ginglymostomatidae) are definitely among the more graceful looking representatives. They characterize a small shark family that is generally quite unknown. The four currently known species are: the Atlantic nurse shark *Ginglymostoma cirratum* (Bonnaterre, 1788), the Tawny nurse shark *Nebrius ferrugineus* (Lesson, 1831), the Shorttail nurse shark *Pseudoginglymostoma brevicaudatum* (Günther, 1867) and, as the most recently described species, the Pacific nurse shark *Ginglymostoma unami* Del Moral-Flores, Ramírez-Antonio, Angulo & Pérez-Ponce de León, 2015 (Ebert *et al.* 2021). In general, nurse sharks are medium-sized, bottom-dwelling and feed mainly on invertebrates and small fish (Ebert *et al.* 2021). Their short, small mouth with large cavities enables them to suck in their prey within milliseconds while searching on the sea floor (Motta *et al.* 2002). Accordingly, the tooth morphology of nurse sharks is unique among all shark species: The teeth are generally almost symmetrical with a triangular shape and have a varying number of small cusplets on both sides of the central cusp. This tooth shape enables them to effectively crack the hard shells of crustaceans, mollusks and other invertebrates, which make up a large part of their prey (Castro 2000).

Representatives of nurse sharks can be found in all of the world's oceans: the Atlantic nurse shark inhabits the western and eastern Atlantic, the Tawny nurse shark the tropical Indian, west and central Pacific Ocean from South Africa to Tahiti and the Shorttail nurse shark can only be found in the waters around Madagascar and East Africa (Ebert *et al.* 2021). The Pacific nurse shark is the only species that inhabits the sea off the American west coast and was classified as a population of the Atlantic nurse shark until a revision in 2015 (Del Moral-Flores *et* *al.* 2015). This previous synonymization distorts the records that had been made about the two species, as data from both species had been included under the Atlantic nurse shark until 2015. Pacific nurse sharks reach a length of about 275 cm (Del Moral-Flores *et al.* 2015).

The tooth morphology of the Pacific nurse shark was published in the first description by Del Moral-Flores *et al.* (2015) and several differences with the Atlantic nurse shark were identified. However, no teeth or jaws from juvenile sharks were examined. We know from records of the Atlantic nurse shark that its tooth morphology changes with maturity (cf. Luer *et al.* 1990; cf. Motta and Wilga 1999; cf. Ebert and Dando 2024), but a similar development has not yet been reported for the Pacific nurse shark. Confirmation of such an ontogenetic change in the Pacific nurse shark could provide valuable insights into the dietary preferences associated with different maturity stages of the species and thus assess the adaptability to varying environmental influences and feeding habits. By comparing these findings with the fossil record of other nurse shark species, it may also become possible to investigate the evolutionary adaptations of nurse sharks to diverse environmental conditions over time.

This study reveals data on the jaw morphology of a juvenile Pacific nurse shark for the first time and explores the tooth development during maturity. Furthermore, the teeth of different nurse shark species were analyzed and their distinguishing features published.

2 | METHODOLOGY

To get an overview of the tooth morphology of a juvenile Pacific nurse shark (*Ginglymostoma unami*), a jaw of this species was examined. The specimen was identified based on a complete individual in accordance with the identification key of the first description by Del Moral-Flores *et al.* (2015). The following identification features were used: (1) Prebranchial length (PG1) 14.5 – 18.0% of total length (TL); (2) the end of the first dorsal fin reaches the insertion of the second dorsal fin; (3) interdorsal space (IDS) 3.6 – 5.6% of TL; (4) the end of the anal fin reaches or exceeds the origin of the lower insertion of the caudal fin; (5) the distance between the axil of the pelvic fins and the beginning of the anal fin comprises less than approximately 1.2 times the base of the first dorsal fin; (6) dermal denticles rhombic with 5 to 6 keels; (7) origin: Eastern Pacific Ocean.

A genetic analysis to compare the individual with a verified specimen of *G. unami* was not performed. However, Del Moral-Flores *et al.* (2015) also refrained from carrying out a genetic analysis to differentiate *G. unami* from *G. cirratum* or other nurse shark species and only relied on the morphological characteristics outlined above. The additional identification feature that the posterior end of the second dorsal fin reaches or is slightly in front of the beginning of the upper lobe of the caudal fin could not be applied in this case, as it is not evident in juvenile animals (Del Moral-Flores *et al.* 2015). Nevertheless, as all other diagnostic features were observable, the identification approach employed here can be considered sufficient, particularly given that Del Moral-Flores *et al.* (2015) also included six juvenile individuals in their morphological analysis.

The jaw was removed from the specimen by dissection. One upper and lower lateral tooth of the right half of the jaw was mechanically removed to allow examination of its lingual side. To remove adhering tissue residues, the teeth were placed in a 10% (m/m) sodium hydroxide solution for 1 hour and then air dried. Fins, skin preparations and vertebras were also removed, dried and stored separately. A small piece of skin from the lateral trunk was removed to investigate the morphology of the dermal denticles.

To compare the tooth morphology of this individual with other nurse sharks (Ginglymostomatidae), representative jaws of the remaining three species were studied. Care was taken to select jaws that show characteristic features of the respective species, to avoid a distorted representation due to intraspecific variation. For this purpose, the general tooth characteristics of all jaws were compared with the following standard literature: Ebert *et al.* (2021) and Compagno (1984, 2002) for *Ginglymostoma cirratum*, *Nebrius ferrugineus* and *Pseudoginglymostoma brevicaudatum*; Luer *et al.* (1990) and Ebert and Dando (2024) for *Ginglymostoma cirratum*; Bass *et al.* (1975) for *Nebrius ferrugineus* and *Pseudoginglymostoma brevicaudatum*. All jaws display the tooth morphology specific to the respective species, as described in the cited literature. To distinguish the three other nurse shark species, the following identification methods were used:

(1) *Ginglymostoma cirratum* (jaw); based on Ebert and Dando (2024): (1) in upper jaw 30 – 42 rows of teeth, in lower jaw 28 – 34 rows; (2) teeth similar in both jaws: erect central cusp flanked by 2 – 6 lateral cusplets; (3) origin: Western or eastern Atlantic Ocean.
The size of the examined jaw (13.3×10.2 cm) and the presence of 3 – 4 well developed cusplets on the distal and mesial edges of all broad-based teeth indicate an adult specimen of this species (cf. Herman *et al.* 1992).

(2) *Nebrius ferrugineus* (jaw); based on Compagno (2002): (1) in upper jaw 29 – 33 rows of teeth, in lower jaw 26 – 28 rows; (2) teeth greatly compressed, with imbricate overlap pattern; (3) tooth crown feet broad, cusps small, three or more moderately large cusplets on each side, and greatly widened basal ledges; (4) origin: Indo-Pacific Ocean.
The large size of the examined jaw (23.7×15.5 cm) and the presence of up to 6 small, well developed cusplets on the distal and mesial edges of all broad-

based teeth indicate an adult specimen of this species (cf. Herman *et al.* 1992).

(3) *Pseudoginglymostoma brevicaudatum* (complete individual); based on Del Moral-Flores *et al.* (2015) and Compagno (2002): (1) short nasal barbels, not reaching the anterior edge of the mouth; (2) second dorsal fin and anal fin similar in size to the first dorsal fin; (3) caudal fin short, less than 20% of TL; (4) origin: Western Indian Ocean.
The total length of the animal (44.5 cm) indicates a subadult specimen, since Ebert *et al.* (2021) listed a total length of approximately 55 – 70 cm for adult females.

Material examined

Ginglymostoma unami. Male. TL 32.5 cm (juvenile). Mexico? (Pacific Ocean). Depth unknown, caught approximately 1950. Coll. J.S. 000T/001-UNB-G/P (private collection). Jaw 4.0 × 3.0 cm (Figure 1A).

Ginglymostoma cirratum. Sex unknown. TL unknown (adult). France (Atlantic Ocean). Depth unknown. Coll. J.S. 001-FRA-G (private collection). Jaw 13.3 × 10.2 cm (Figure 1B).

Nebrius ferrugineus. Sex unknown. TL unknown (adult). Philippines (Pacific Ocean). Depth unknown. Coll. J.S. 001-PHL-G (private collection). Jaw 23.7 × 15.5 cm (Figure 1C).

Pseudoginglymostoma brevicaudatum. Female. TL 44.5 cm (subadult). Madagascar (Indian Ocean). Depth unknown. Coll. J.S. 000T/001-MDG-G/P (private collection). Jaw 5.8 × 4.4 cm (Figure 1D).

The photos were taken with the following equipment and parameters: Sony DSC-TX30, no magnification (Figure 1, 2 and 4); magnification mode “Lupe Plus” (Figure 5, 9 and 10); INSKAM Digital Microscope Model 1600, varying magnification (Figure 3A, 6, 8 and 11) and AmScope T390B optical microscope, magnification 10 × 10 (Figure 3B, 3C and 3D). The selection of equipment and imaging parameters was guided by the objective of achieving comparable image quality across the respective specimens. In cases where figures consisted of multiple images (Figures 8, 9, 10 and 11), a consistent magnification level was maintained throughout. Higher magnification settings were employed as necessary to capture increased levels of morphological detail. The original image resolutions were sufficient to visualize all tooth morphological features described in association with the corresponding figures (3206 × 2404 pixels for the Sony DSC-TX30; 1280 × 720 pixels for the INSKAM Digital Microscope Model 1600 and 1280 × 1024 pixels for the AmScope T390B optical microscope). All external measurements follow the descriptions of Compagno (1984) and were measured with a caliper to an accuracy of 1 mm.

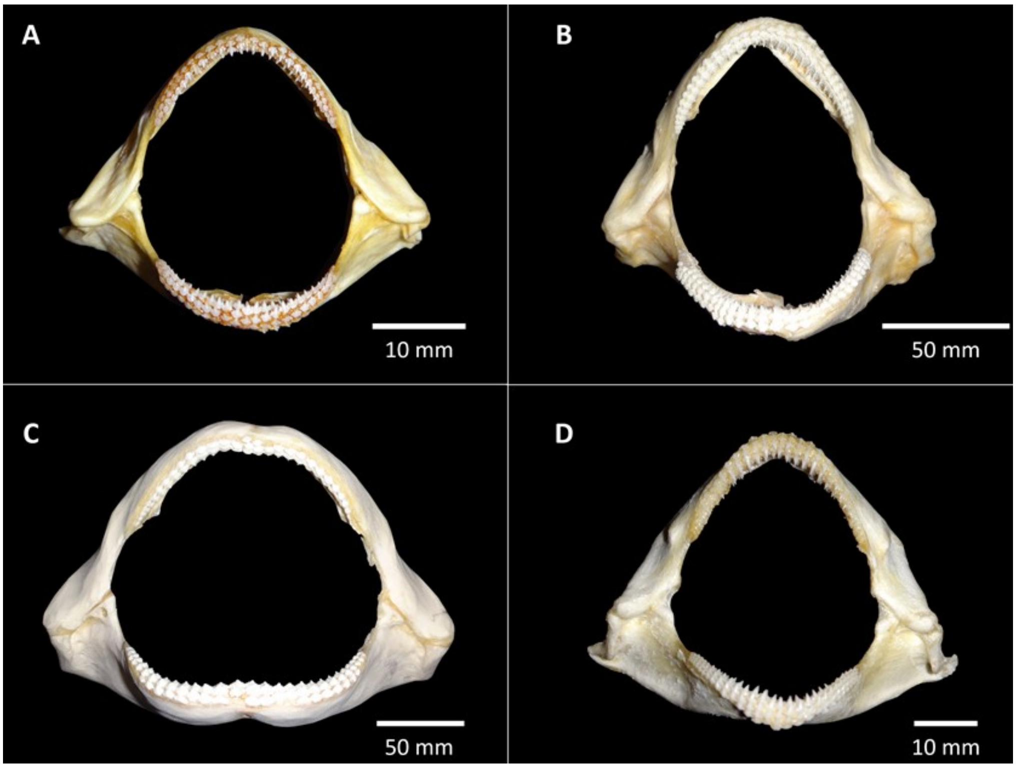

FIGURE 1 Examined jaws of the four nurse shark species: *Ginglymostoma unami* 000T-UNB-G. (A), *Ginglymostoma cirratum* 001-FRA-G. (B), *Nebrius ferrugineus* 001-PHL-G. (C) and *Pseudoginglymostoma brevicaudatum* 000T-MDG-G. (D).

3 | RESULTS AND DISCUSSION

3.1 Identification

The individual was measured according to the methods listed and compared with the data of Del Moral-Flores *et al.* (2015). An overview of the measured parameters is listed in Table 1 and Figure 2. *Ginglymostoma unami* differs from *G. cirratum* by the following criteria: prebranchial length (PG1) 14.5 – 18.0% of TL vs. 12.0 – 15.0% of TL; interdorsal space (IDS) 3.6 – 5.6% of TL vs. 5.4 – 9.5% of TL; The end of the first dorsal fin does (vs. does not) reach the insertion of the second dorsal fin; The distance between the axil of the pelvic fins and the beginning of the anal fin comprises less than approximately 1.2 times the base of the first dorsal fin (vs. more than 1.4 times); Dermal denticles rhombic with 5 to 6 keels vs. elongated with less than 5 keels; Origin: Eastern Pacific Ocean vs. Atlantic Ocean (Del Moral-Flores *et al.* 2015).

TABLE 1 Comparison of the identification-specific measurement data of the examined specimen of *Ginglymostoma unami* with three neonate and immature paratypes of Del Moral-Flores *et al.* (2015).

Measurements	Examined specimen (male)		CNPE-IBUNAM 9492 (male)		UCR 25-16 (female)		UCR 200-33 (male)		General range* (% TL)
	cm	% TL	cm	% TL	cm	% TL	cm	% TL	
Total length (TL)	32.5	100.0	49.5	100.0	27.4	100.0	37.3	100.0	/
Prebranchial length (PG1)	5.1	15.7	8.4	17.0	4.9	18.0	6.3	16.7	14.5–18.0
Interdorsal space (IDS)	1.5	4.6	2.5	5.1	1.0	3.6	1.9	5.1	3.6–5.6
First dorsal fin base (D1B)	3.6	11.1	4.9	9.9	2.5	9.0	3.4	9.2	9.0–12.3
Pelvic-anal space (PAS)	4.2	12.9	5.8	11.7	3.1	11.4	4.3	11.5	10.2–14.2
PAS / D1B	1.17		1.18		1.24		1.26		1.04–1.26

* The general range refers to all examined specimens of *G. unami* described by Del Moral-Flores *et al.* (2015). The general range of PAS / D1B is dimensionless and not given in % TL.

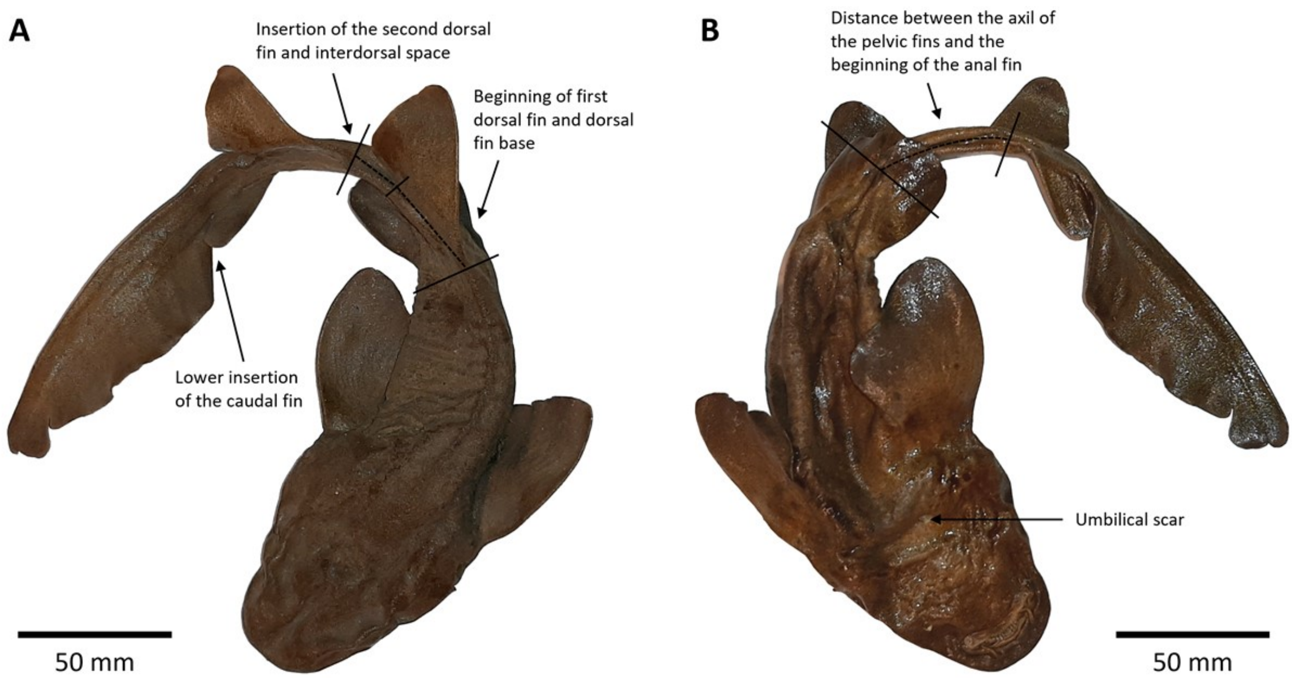

FIGURE 2 Examined specimen of *Ginglymostoma unami* before dissection with marked identification features 2, 3, 4 and 5.

The dermal denticles located on the lateral trunk of the examined specimen are broad, rhombic and exhibit 5 to 6 keels (Figure 3). This morphology corresponds to the description provided by Del Moral-Flores *et al.* (2015), and differs from that observed in *G. cirratum*, as previously noted. The denticles have an average size of approximately 300 × 200 µm. Apart from their smaller dimensions, the denticle morphology does not deviate from the depiction by Del Moral-Flores *et al.* (2015). However, it must be noted that the specimen examined in this study had been treated with a glue-like substance during earlier preservation efforts, which could not be fully removed. Consequently, only a limited number of dermal denticles were suitable for more detailed examination. Del Moral-Flores *et al.* (2015) did not specify the precise position of the denticles shown in their study, and it is well established that dermal denticle morphology can vary substantially, even within a single individual (Dillon *et al.* 2017). Therefore, it cannot be ruled out that their morphology can also differ from the previously known characteristics in other body parts of *G. unami* and further studies are needed to investigate this possibility.

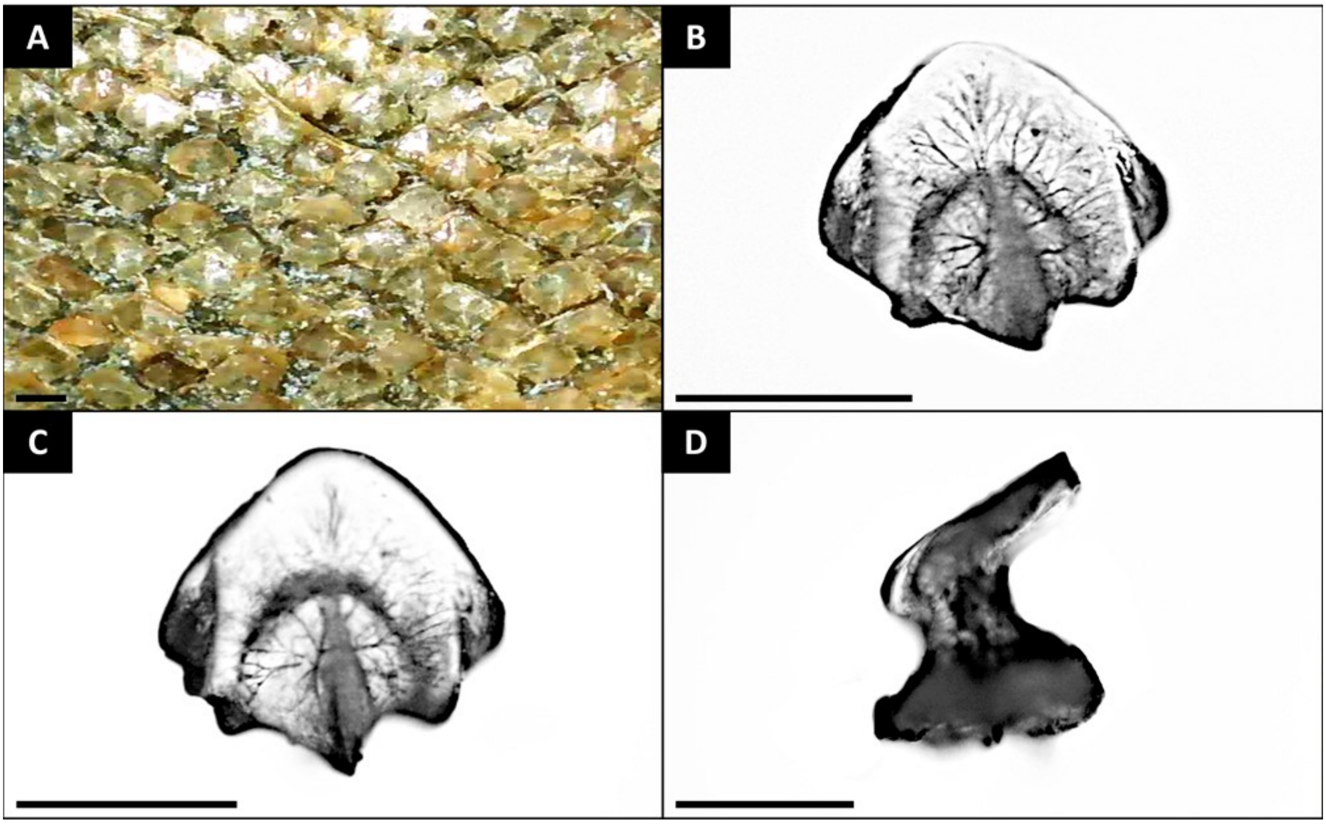

FIGURE 3 Broad, rhombic dermal denticles of the lateral trunk of the *Ginglymostoma unami* specimen examined, which show 5 to 6 keels: Overview (A), apical view of the crown (B, C) and lateral view (D). Each scale bar is 200 µm.

3.2 Tooth count and morphology

The teeth in the upper and lower jaw have the same morphology (dignathic homodonty) and exhibit a broad-based, but relatively high and elongated principal cusp (Figure 4 and 5). The maximum tooth height is 1 mm. In anterior teeth, the cusp is erect and symmetrical (Figure 6A and 6D), gradually becoming weakly inclined toward the lateral and anterior teeth (Figure 6B and 6E). The main cusp has almost straight cutting edges, which can be slightly concave in anterior and slightly convex in posterior teeth. The mesial and distal cutting edges feature 1 – 2 relatively large, rounded cusplets next to the central cusp, which do not exceed half of the maximum height of the tooth. Otherwise, the teeth are smooth-edged and have no serrations. The last posterior teeth have only a very weakly developed crown, where the cusps are barely recognizable (Figure 6C and 6F).

A broad apron is present at the central labial base of the crown, overhanging the crown-root junction. It is flattened and arched in the labial direction. On the lingual base, a prominent uvula is situated. It is narrower than the apron but extends just as far in the lingual direction, as the apron in the labial direction and divides the tooth into a mesial and a distal half. The root is divided into two lobes, which are not visible when the teeth are naturally positioned in the jaw. On the lingual side of the root there is a pronounced central foramen, which is surrounded by smaller foramina on the root lobes. The tooth morphology corresponds to the records of Herman *et al.* (1992), who provided detailed microscopic images of some isolated teeth of a juvenile *G. unami*, although he attributed them to *G. cirratum*. There is a total of 6 consecutive tooth rows in the upper and lower jaw. Del Moral-Flores *et al.* (2015) illustrated the teeth of *G. unami* as small with a central cusp symmetrically bordered by 4 or more cusplets and a tooth formula of 13 to 15-1-13 to 15 / 16 to 18-0-16 to 18. Sexual dimorphism regarding tooth morphology has not been described for this species (Del Moral-Flores *et al.* 2015).

FIGURE 4 Jaw of the examined juvenile specimen of *Ginglymostoma unami*. The image shows the correct position of the teeth.

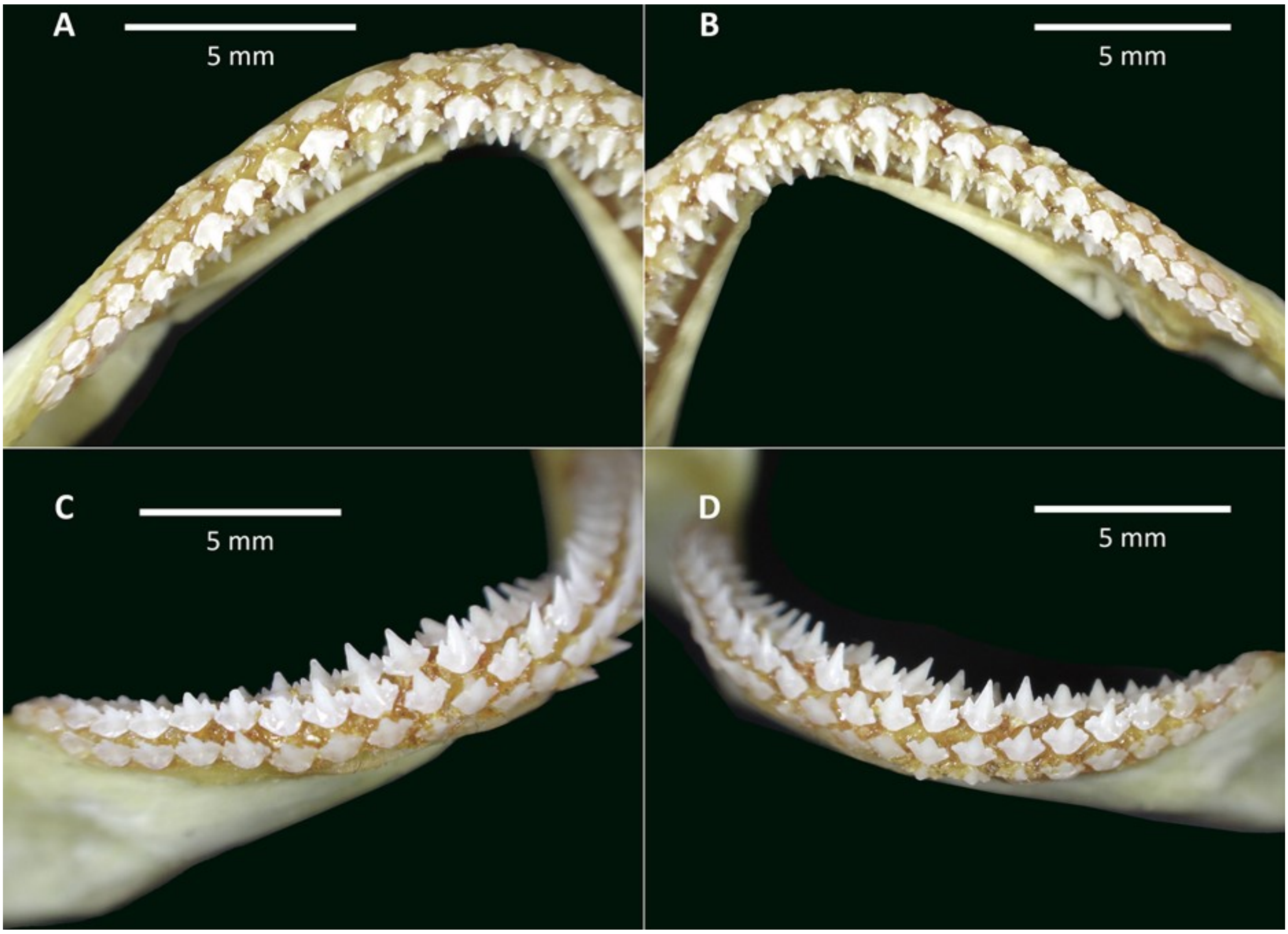

FIGURE 5 Left upper jaw (A), right upper jaw (B), left lower jaw (C) and right lower jaw (D) of the examined juvenile specimen of *Ginglymostoma unami*. The images show the correct position of the teeth.

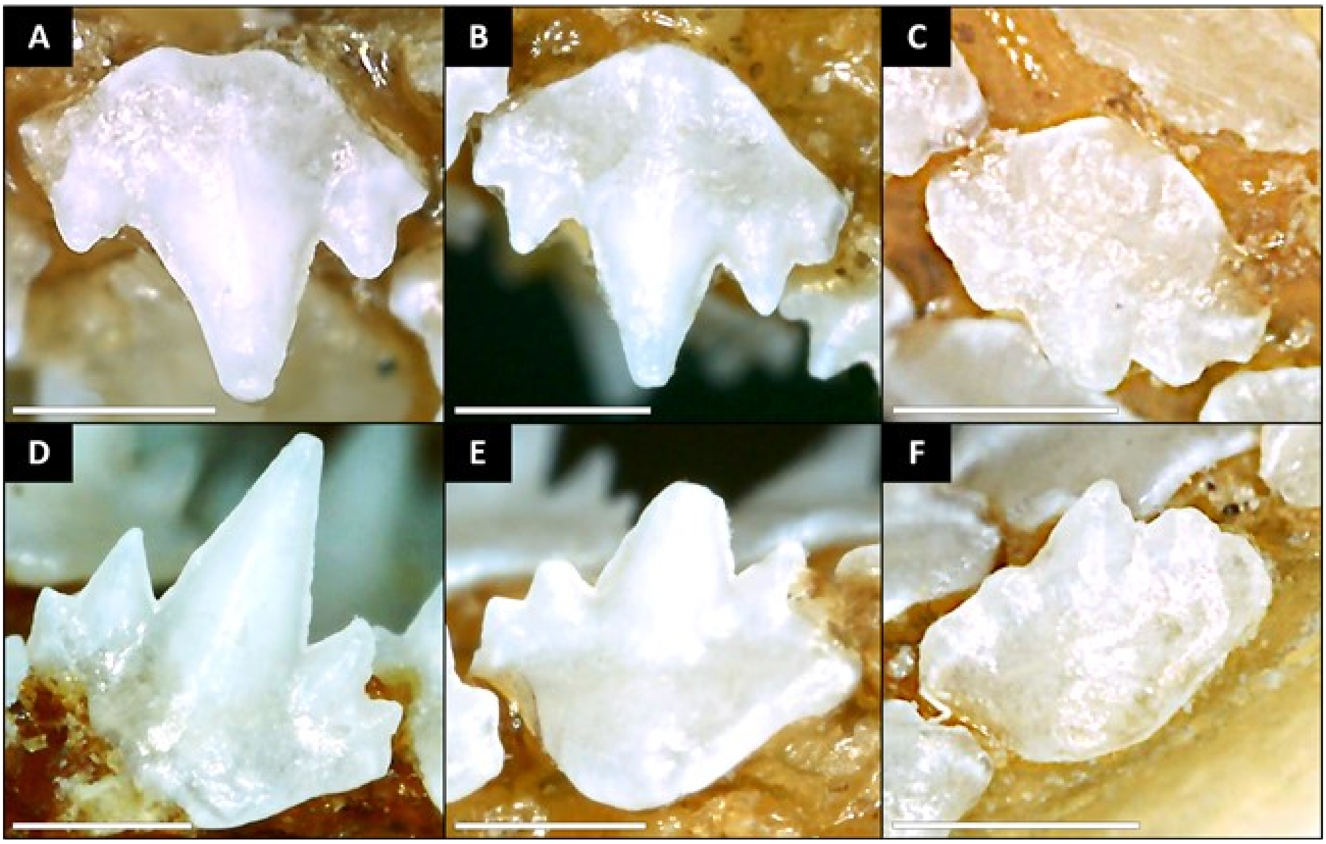

FIGURE 6 Anterior upper (A) and lower tooth (D); lateral upper (B) and lower tooth (E); posterior upper (C) and lower tooth (F) of the examined juvenile specimen of *Ginglymostoma unami*. The images show the correct position of the teeth. Each scale bar is 500 µm.

The depiction of the tooth morphology in the first description differs from the teeth of the examined individual, where only a maximum of 2 cusplets are visible on the sides of the central cusp; the tooth formula also deviates (14-1-15 / 12-1-12). Del Moral-Flores *et al.* (2015) noted that the tooth formula in immature individuals can differ by 1-3 teeth, but the aberration considered here is slightly outside these limits (deviation of four teeth in one half of the lower jaw). However, this is not surprising, since Del Moral-Flores *et al.* (2015) only included six immature individuals in the study. The difference can therefore be explained by intra-specific variation, which previously went unnoticed due to the small sample size. The observations of the specimen examined and the data from Del Moral-Flores *et al.* (2015) prove that juvenile Pacific nurse sharks have fewer tooth rows than adults. This is especially important for distinguishing nurse sharks of different species and sexual maturity, since the tooth formula can be used as an identification feature; explicitly when comparing isolated jaws (Ebert *et al.* 2021). To ensure a valid identification, it is important to continually update the available tooth formulas for the different species as new information becomes available. The corrected tooth formula for *G. unami* taking the data of the examined specimen into account, is as follows: 13 to 15-1-13 to 15 / 12 to 18-0 to 1-12 to 18 (27 to 31 / 24 to 37 respectively).

The observed different tooth morphology can be explained by the maturity of the animal, as Del Moral-Flores *et al.* (2015) included images of the teeth of an adult animal. These images correspond to their description and allow us to conclude the development of the tooth morphology from juvenile Pacific nurse sharks (*G. unami*) to the adult stage: The previously more pointed and higher teeth with 1 to 2 larger cusplets develop into broader teeth with 4 or more smaller cusplets over the course of life (Figure 7). This development has already been observed in Atlantic nurse sharks, *G. cirratum* (cf. Luer *et al.* 1990; cf. Motta and Wilga 1999; cf. Ebert and Dando 2024). It was therefore likely that this also occurs in their Pacific relatives, which has been confirmed here.

3.3 Comparison with other nurse shark species

The tooth morphology of both *Ginglymostoma* species differs greatly from that of their two relatives. While *Nebrius ferrugineus* has nearly comb-like teeth, with broad crown feet, small central cusps and three or more moderately large cusplets on each side of the central cusp (Figure 8), *Pseudoginglymostoma brevicaud*atum has pointed teeth with only 1 or 2 cusplets (Figure 9). The teeth of the latter species are more reminiscent of *Stegostoma tigrinum* Forster, 1781 than other nurse shark species (cf. Bass *et al.* 1975).

Since no jaw of an adult *G. unami* could be examined in this study and no juvenile jaws of *G. cirratum* were available, it cannot be confirmed with certainty that these two species can be distinguished exclusively based on their tooth morphology. Del Moral-Flores *et al.* (2015) listed that there are differences in the tooth morphology in comparison to *G. cirratum*: The teeth of *G. unami* are flat and blunt rather than pointed and sharp in comparison to *G. cirratum*. Moreover, *G. unami* has a greater number of cusplets arranged symmetrically with respect to the central cusp. The mentioned features cannot be confirmed or revised for the time of this study, since there is not enough data on the tooth morphology of different *G. unami* individuals. It cannot be excluded that these characteristics are merely intraspecific variation, a dependence on maturity or sex. Further scientific data is needed to answer this question with certainty. Nevertheless, a graphic comparison of the tooth morphology of the examined juvenile *G. unami* and an adult *G. cirratum* is given (Figure 10 and 11). The teeth of an adult *G. cirratum* show around 4 cusplets on each side of the central cusp (Figure 11).

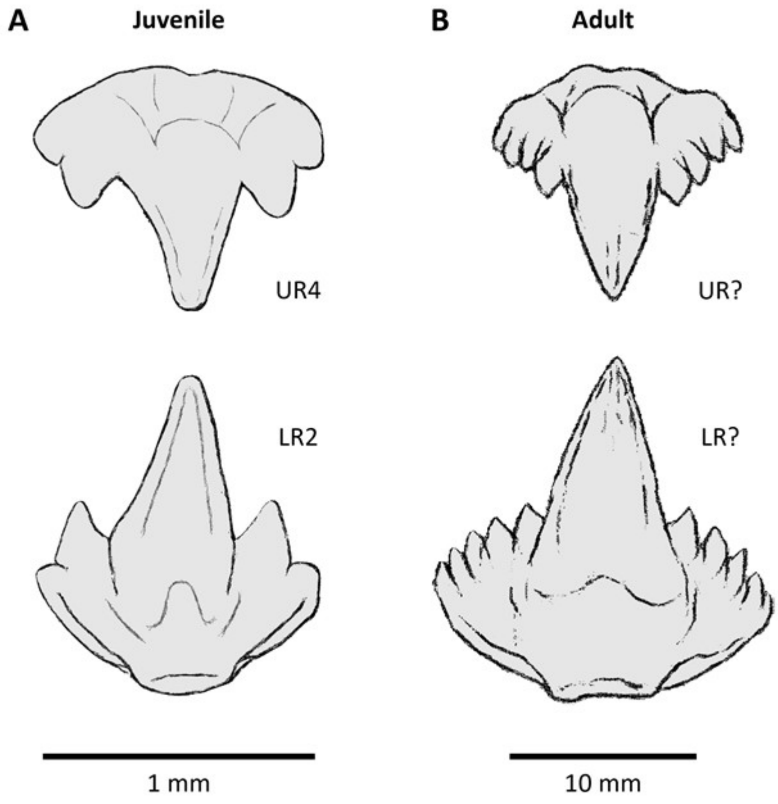

FIGURE 7 Comparison of the lateral teeth of a juvenile (A) and an adult specimen (B) of *Ginglymostoma unami*. Juvenile specimens have higher teeth compared to their base width, with 1-2 large cusplets on each side, while teeth of adults have broader teeth with 4 or more cusplets. Teeth of adult *G. unami* published by Ebert *et al.* (2021); modified.

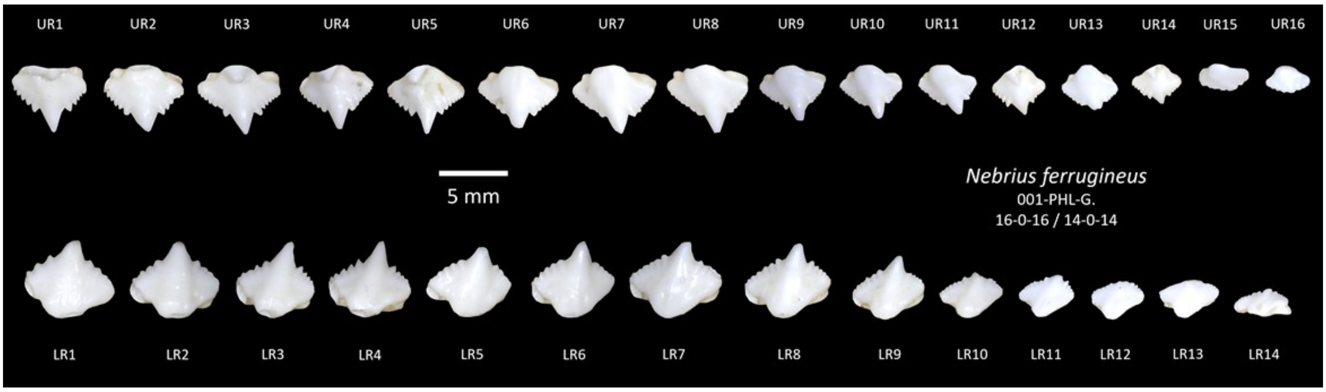

FIGURE 8 Dentition of *Nebrius ferrugineus* specimen 001-PHL-G (right upper and lower jaw). The image shows the correct position of the teeth.

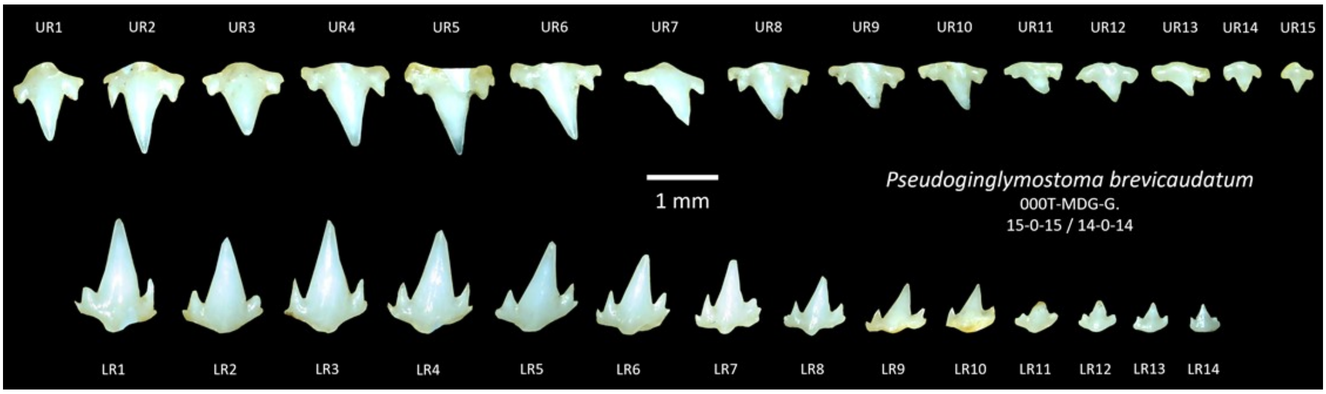

FIGURE 9 Dentition of *Pseudoginglymostoma brevicaudatum* specimen 000T-MDG-G (right upper and lower jaw). The image shows the correct position of the teeth.

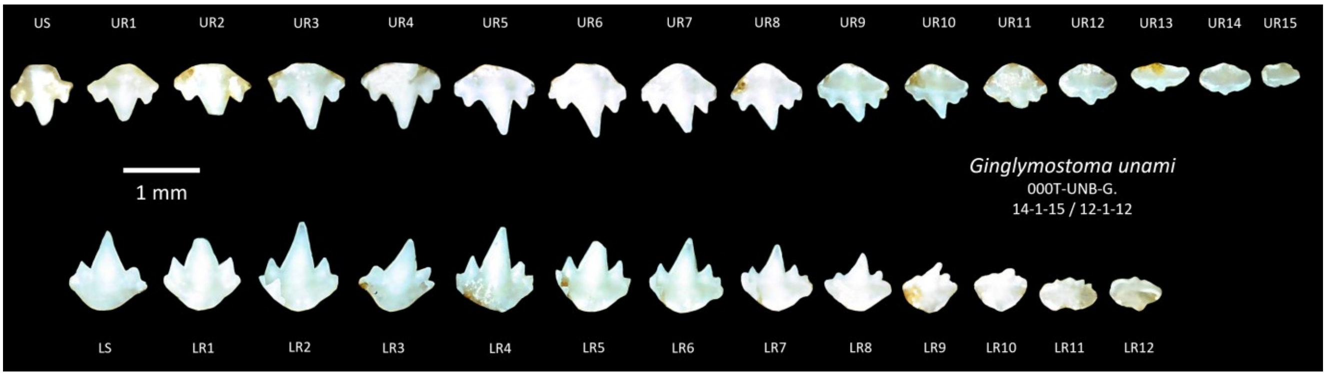

FIGURE 10 Dentition of *Ginglymostoma unami* specimen 000T-UNB-G (right upper and lower jaw). The image shows the correct position of the teeth.

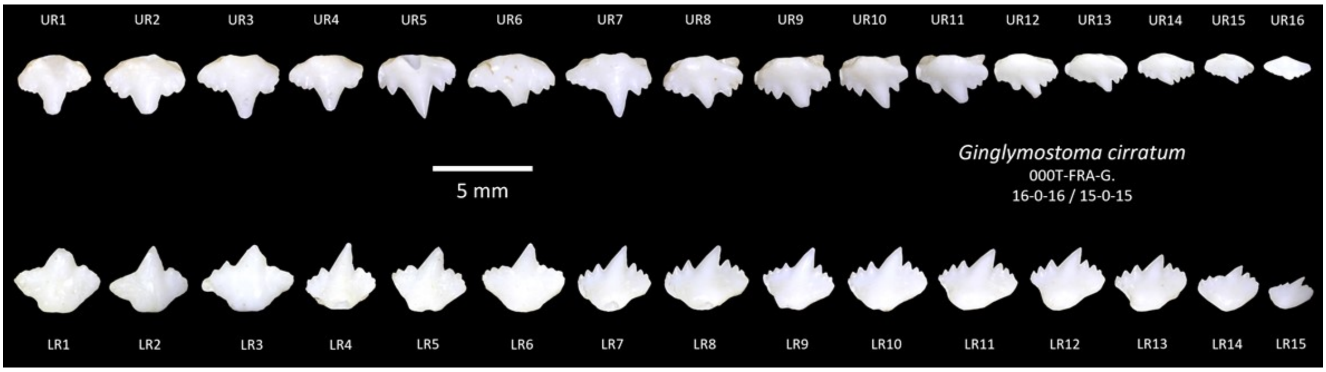

FIGURE 11 Dentition of *Ginglymostoma cirratum* specimen 000T-FRA-G (right upper and lower jaw). The image shows the correct position of the teeth.

4 | CONCLUSIONS

This study illustrated the jaw and tooth morphology of a juvenile Pacific nurse shark (*G. unami*) for the first time and describes their change over the course of life, as previously observed in the Atlantic nurse shark (*G. cirratum*). The teeth of juvenile individuals are higher in relation to their width and have only a few cusplets, while in adult animals they are broader and have significantly more cusplets. In addition, adults have more tooth rows per jaw half than juvenile individuals. We can only speculate about the advantages of this development. It is conceivable that juvenile sharks may have a different prey spectrum compared to adults. The pointier teeth could be better suited for catching small fish, but less for cracking the hard shells of mollusks and crustaceans. As no studies to date have addressed the diet of juvenile Pacific nurse sharks, the hypothesis of an ontogenetic change in prey spectrum remains highly hypothetical. To substantiate this assumption and to establish a reliable correlation between tooth morphology and feeding behavior, further investigations involving a larger number of examined specimens and in situ observations of living individuals in their natural environment are required.

Finally, this study underscores the considerable gaps that remain in our understanding of nurse sharks and elasmobranchs in general. All known nurse shark species are currently classified as Vulnerable, Endangered or Critically Endangered by the IUCN. A clearer understanding of the relationship between tooth morphology and dietary preferences may provide crucial insights into the ecological adaptability of these species to shifting environmental conditions.

Should the hypothesis be confirmed in the future, that juvenile Pacific nurse sharks feed on different diets than adults, the loss of a specific food source (whether due to overfishing or climate change) could critically affect a particular ontogenetic stage. Given the morphological specialization of their dentition and corresponding dietary habits, these sharks would likely be unable to adapt rapidly to alternative prey sources, rendering them highly susceptible to ecological disturbances. Eventually, the survival of the species would be seriously threatened, as the decimation of both the juvenile and the adult generation could lead to the extinction of the entire species due to the lack of animals of reproductive age. Therefore, elucidating the link between tooth morphology and diet in relation to sexual maturity is essential for developing effective conservation strategies for the Pacific nurse shark.

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CONFLICT OF INTEREST

The author declares no conflict of interest.

ETHICAL APPROVAL

The content of this study complies with all regulations of the German Animal Welfare Act (TierSchG) and the Federal Nature Conservation Act (BNatSchG). All specimens used were collected and imported legally. None of them are protected by the Washington Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) at the time of this study. In compliance with the laws and regulations mentioned, no further ethical or legal approval is required for handling these species.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on a reasonable request from the corresponding author.

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