



**The report of a rare deformed eagle ray
(Myliobatiformes: Myliobatidae)
tooth plate from the Neogene of Calvert Cliffs, Maryland, U.S.A.**

Stephen J. GODFREY^{1, 2}

David J. BOHASKA^{2, 3}

John MAISEY⁴

Abstract: An isolated and deformed lower tooth plate of an eagle ray (*Aetomylaeus* sp., Myliobatidae, Myliobatiformes) is reported herein from the Miocene deposits along Calvert Cliffs, Maryland, U.S.A. Deformed myliobatid tooth plates like this, either fossil or modern, are exceedingly rare. All medial teeth are deformed/skewed such that the right side of each tooth forms an angle of about 10 degrees to the transverse axis of the dental plate. The skewed abnormal form of the teeth in USNM PAL 726325 is not thought to be the result of modern or taphonomic deformation. Rather, the deformity exhibited by USNM PAL 726325 gives every indication that successive similarly deformed teeth came about as a result of a persistent anatomical deformity of the dental lamina. From the consistency in the deformed shape of each tooth, it would appear as though the dental lamina retained this anomalous shape at least throughout the time represented by the age of the tooth plate. If this interpretation is correct, the deformity was not fatal and did not significantly impair the functionality of the tooth pavement over a protracted part (or all) of the individual's life span.

Key-words:

- deformed dental lamina;
- eagle ray;
- *Aetomylaeus*;
- Myliobatidae;
- Miocene;
- Calvert Cliffs

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Résumé : *Description d'un rare palet dentaire déformé de raie aigle de mer (Myliobatiformes : Myliobatidae) du Néogène de Calvert Cliffs, Maryland, États-Unis d'Amérique.*- Un palet dentaire inférieur, isolé et déformé, d'une raie aigle de mer (*Aetomylaeus* sp., Myliobatidae, Myliobatiformes) décrit ici provient d'un affleurement miocène des Calvert Cliffs, Maryland, États-Unis d'Amérique. Les palets dentaires déformés de myliobatides tels que celui-ci, qu'ils soient fossiles ou actuels, sont extrêmement rares. Toutes les dents mésiales sont déformées ou asymétriques, de telle manière que le côté droit de chaque dent forme un angle d'environ 10 degrés sur l'axe transverse du palet dentaire. La forme anormale asymétrique de la dent USNM PAL 726325 n'est pas considérée comme résultant d'une déformation taphonomique ou actuelle. Mais la déformation présentée par USNM PAL 726325 indiquerait plutôt que des dents successives, pareillement déformées, surviennent comme le résultat d'une déformation anatomique récidivante du palet dentaire. D'après la constance de la silhouette déformée de chaque dent, il apparaîtrait que le palet dentaire a conservé sa forme anormale au moins au cours de la période représentée par l'âge de la plaque dentaire. Si cette interprétation est juste, cette difformité n'était pas fatale et n'handicapait pas de manière significative la fonctionnalité du pavage dentaire pendant une partie notable de (voire toute) l'espérance de vie de l'individu.

¹ Department of Paleontology, Calvert Marine Museum, P.O. Box 97, Solomons, MD 20688 (U.S.A.)

Stephen.Godfrey@calvertcountymd.gov

² Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC, 20013-7012 (U.S.A.)

³ bohaskad@si.edu

⁴ Department of Vertebrate Paleontology, American Museum of Natural History, 200 Central Park West, New York, NY 10024 (U.S.A.)

maisey@amnh.org



**Mots-clefs :**

- palet dentaire déformé ;
- raie aigle de mer ;
- *Aetomylaeus* ;
- Myliobatidae ;
- Miocène ;
- Calvert Cliffs

1. Introduction and setting

In the case study presented here, we describe a Miocene epoch lower tooth plate of the extant myliobatid genus, *Aetomylaeus* sp. GARMAN, 1908, that exhibits a right-side anteriorly-skewed medial tooth deformity. Anomalous dentitions like this are exceedingly rare in rays in general and hitherto have only been described in three specimens figured by HOVESTADT and HOVESTADT-EULER (2013, see below). These latter specimens are not deformed to the same degree as the one featured herein. Our aim is not merely to document such an occurrence in this taxon, but also to highlight the extent to which such a deformity can affect replacement tooth formation.

Eagle rays are large aquilopelagic (forms with wing-like discs) chondrichthyans that are powerful swimmers and durophagous predators consuming gastropods and bivalves, as well as decapod crustaceans (LAST *et al.*, 2016). They have rigid jaws and large muscles that generate bite forces capable of fracturing mollusk shells (KOLMANN *et al.*, 2015; VILLAFANA *et al.*, 2019). Eagle rays of the genus *Aetomylaeus* are known from the late Eocene to the present (VILLAFANA *et al.*, 2019). However, they are most common in the Neogene (CARRILLO-BRICEÑO *et al.*, 2019; VILLAFANA *et al.*, 2019). VILLAFANA *et al.* (2019) provide a detailed listing of where geographically, and when geologically specimens attributed to *Aetomylaeus* have been found. *Aetomylaeus* is the sole myliobatid known from the fossil-rich Calvert Cliffs (Miocene, Chesapeake Group) located along the western shore of Chesapeake Bay (Fig. 1) in Calvert County, Maryland, U.S.A. (KENT, 2018) [Note that KENT (2018) mentioned two myliobatid genera, *i.e.*, *Pteromylaeus* and *Aetobatus*. Now however, *Pteromylaeus* = *Aetomylaeus*, and *Aetobatus* has been transferred to the Aetobatidae].

The dentition of *Aetomylaeus* spp. consists of flat-crowned teeth that interlock to form pavement-like tooth plates (CAPPETTA, 2012, Fig. 441 F; HOVESTADT and HOVESTADT-EULER, 2013; KOLMANN *et al.*, 2015, Fig. 1; KENT, 2018, Fig. 2.25; MARRAMÀ *et al.*, 2019, Fig. S4b). Each tooth forms from a continuous dental lamina, with new teeth developing through a conveyor belt-like replacement mechanism (UNDERWOOD *et al.*, 2015; RASCH *et al.*, 2020). In *Aetomylaeus*, individual upper and lower teeth are not distinct morphologically (CAPPETTA, 2012; KENT,

2018, Fig. 2.25; MARRAMÀ *et al.*, 2019, Fig. S4b). However, upper and lower tooth pavements can be distinguished on the basis of their anteroposterior curvature (HOVESTADT and HOVESTADT-EULER, 2013, Pl. 14; KOLMANN *et al.*, 2015, Fig. 1, sagittal view). Lower tooth pavements are nearly flat to only gently convex dorsally (like the one described herein), whereas upper dentitions are much more strongly convex dorsally from front to back (KOLMANN *et al.*, 2015, Fig. 1, sagittal view; VILLAFANA *et al.*, 2019, Fig. 2a). Only the anterior parts of the upper and lower tooth plates occlude to form a functional grinding pad, as evidenced by the wear pattern visible on the tooth plate (Figs. 2-3).

2. Materials and methods

USNM PAL 726325, Department of Paleobiology collections, National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A. Tooth terminology follows CAPPETTA (2012).

There was no sediment adhering to the three pieces of the mouth plate when they were found. Polyvinyl butyral in acetone was used to glue the three pieces together, but otherwise, no consolidant was applied to the specimen. In its natural state, USNM PAL 726325 is nearly jet black (Fig. 2.B), so to improve contrast and visibility (Fig. 2.A), the mouth plate was lightly dusted with sublimed ammonium chloride (a whitening technique described by COOPER (1935) and FELDMAN (1989)). After the specimen was photographed with a Nikon Coolpix P510 camera on black velvet under fluorescent light, the ammonium chloride was removed by holding the specimen under running water (SHELBURNE & THOMPSON, 2016). As a cautionary note, specimens coated with ammonium chloride should be stable enough to withstand a fresh water rinse because without that, there would be the possibility of a residue of hydrochloric acid (HCl) left on the specimens if they are not washed thoroughly.

The images were edited in Adobe Photoshop® and compiled in Adobe Illustrator®.

3. Geology

USNM PAL 726325 was not found *in situ*. Rather, it was found in three pieces on the beach over a two-month period. The first piece was found by author D.J.B. on 14 January 2018, 85 m north of the "waterfall", high on the beach. In a form going back to at least Remington KELLOGG, this is 85 m north of the south end of the third cliff south of the mouth of Parkers Creek, Port Republic, Calvert County, Maryland (Fig. 1). Approximate GPS coordinates are: N 38°31.797' W 076°30.970'.



Figure 1: Satellite image (insert) of Eastern North America and below a portion of the northern section of Chesapeake Bay and parts of the States of Maryland and Virginia. The one black dot (immediately south of Parkers Creek, Calvert County, MD) marks the location where the Miocene stingray pathological mouthplate was found. Modified from VOGT *et al.* (2018).



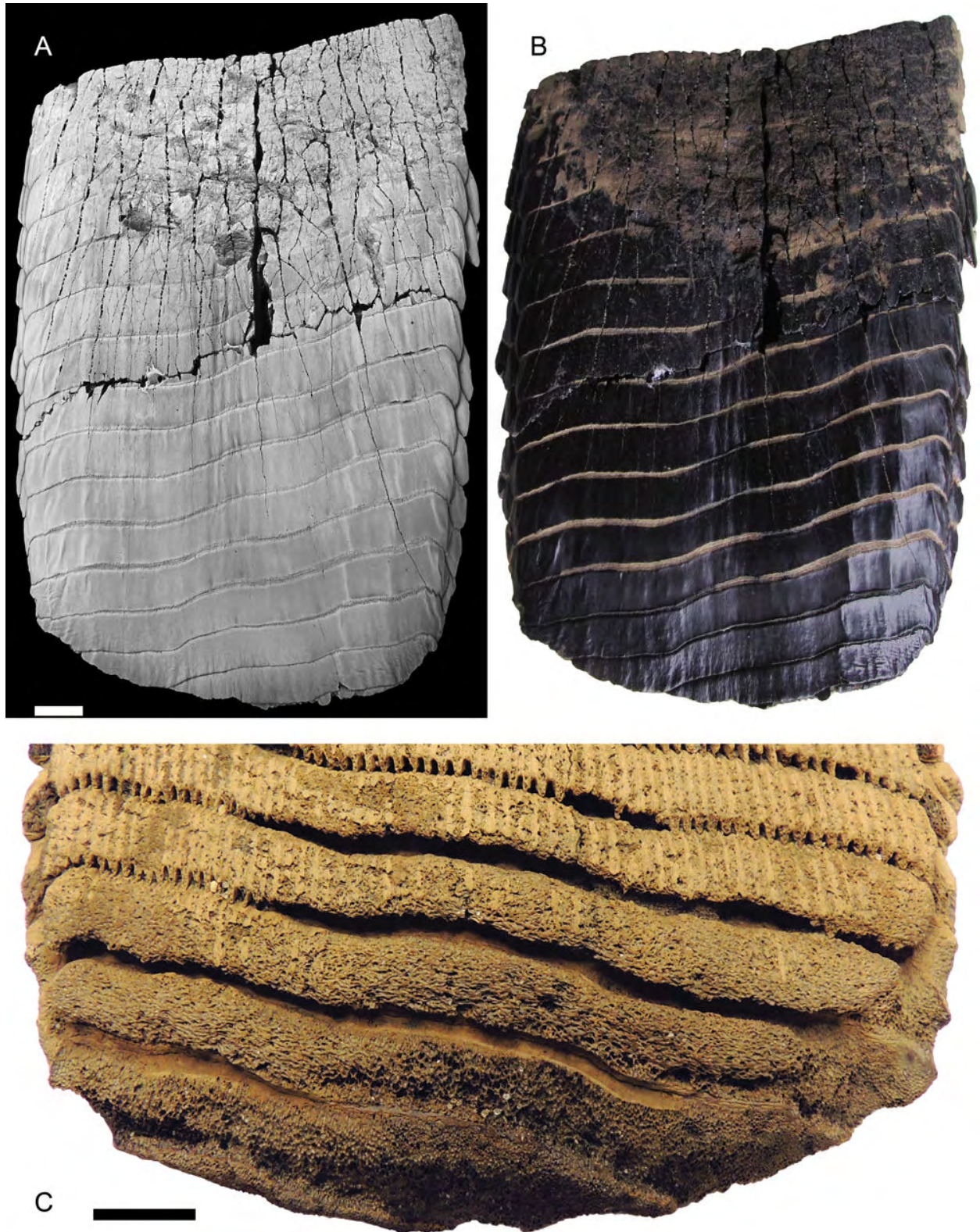


Figure 2: USNM PAL 726325 eagle ray (*Aetomylaeus* sp.) partial tooth plate. A and B are both occlusal views. A. Specimen whitened with sublimed ammonium chloride to highlight surface detail. C. Posterior margin of the tooth plate in a basal view. Scale bars equal 10 mm.

In an occlusal view of the dental plate, this piece comprises the upper left quarter. The second piece was found on 20 January 2018, 17 m north of the "waterfall", in the water, in gravel, at the water's edge. Approximate GPS coordinates are: N 38°31.767', W 076°30.955'.

Therefore, the two pieces were found approximately 72 m apart. This is the largest piece comprising the lower half of the plate. The third piece (upper right) was apparently found in the same area by Joseph CUMBERLAND, 11 February 2018.



These pieces of the dental plate were beach-float long enough for any adhering matrix to wash off. Determination of source bed from lithology or microfossils is therefore not possible. Given their sizes and good preservational condition, the pieces probably did not travel far from their originating position in the cliffs. In the immediate area where USNM PAL 726325 was found, only Shattuck-Zones 11-19 are exposed in the cliffs, which includes the upper portion of the Plum Point Member (Shattuck-Zones 11-15) of the Calvert Formation along with the Drumcliff (Shattuck-Zone 17), St. Leonard (Shattuck-Zone 18), and Boston Cliff (Shattuck-Zone 19) members of the Choptank Formation (KIDWELL *et al.*, 2015, Fig. 15). KENT (2018) recently compiled a detailed review of the diverse chondrichthyan fauna known from Calvert Cliffs. *Aetomylaeus* (= *Pteromylaeus*) has been reported (KENT, 2018, p. 128) *in situ* in various (but not all) Shattuck-Zones 1 through 23, including 11-12, 14, 17, 19, which cover the span of Shattuck-Zones in the adjacent cliff section, as well as sections north and south. We therefore conclude that USNM PAL 726325 originated from within Shattuck-Zones 11 through 19, but cannot restrict it further. The sediments comprising this section of the cliffs range in age between approximately 16.5-12.5 Ma (PEREZ *et al.*, 2019, Fig. 1). KIDWELL *et al.* (2015, and references therein) provide a detailed description of the geology of the cliffs and VOGT *et al.* (2018) give an overview of the very diverse Miocene (mostly marine) biota that is preserved along Calvert Cliffs.

4. Description

USNM PAL 726325 consists of a lower dental plate that has a maximum midline length and width of 135 mm and 101 mm respectively. Some small fragments are missing where the plate broke apart. There is a shallow longitudinal concavity medially that extends the full length of the tooth plate, as opposed to the convex surface expected. The dental plate consists mostly of 15 elongate medial teeth (= symphyseal teeth; UNDERWOOD *et al.*, 2015), the posterior three of which are not complete width-wise (Figs. 2-3). It is not known how many more medial teeth may have been present in life. A smaller number of lateral teeth are preserved. They are much shorter width-wise and lozenge-shaped, but otherwise have a structure comparable to that of the medial teeth (HOVESTADT & HOVESTADT-EULER, 2013; KENT, 2018; VILLAFANA *et al.*, 2019). Although many lateral teeth are missing, at two positions on the left and one right, two files of teeth are present. There were therefore at least five tooth files in this individual.

The medial teeth are over nine times wider than long (a characteristic of the genus *Aetomylaeus*), whereas teeth of *Myliobatis* are only

four to five times wider than long (KENT, 2018). The maximum width of the anterior-most medial tooth (as measured along the width of the skewed tooth) is 98.5 mm, whereas the same dimension of the posterior-most complete tooth is 94.5 mm. Therefore, the medial teeth decrease in width by 4 mm from front to back.

The surface of the medial tooth crowns is lightly ornamented, mostly with labiolingually oriented low ridges, more numerous and conspicuously developed laterally (Fig. 2.A-B). The roots of fully formed teeth are polyaulacorhizous, with 65 fine, labiolingually directed laminae separating the nutritive groves (Fig. 2.C). The occlusal surface at the anterior end of the dental plate preserves a semi-circular wear pattern (Figs. 2.A-B, 3) that presumably developed in life where opposing dentitions crushed prey.

In an occlusal view of a normal tooth plate (KENT, 2018, Fig. 2.25), a line passing through the maximum width of each medial tooth would be orthogonal to the long axis of the plate. However, in USNM PAL 726325, adjacent medial teeth are skewed such that the right side of each tooth forms an angle of about 10 degrees to the transverse axis of the dental plate (Figs. 2-3).

In a basal view of the posterior margin of the dental plate (Fig. 2.C), parts of four incomplete (widthwise) teeth are preserved. Although the occlusal surface of these teeth gives every appearance of having been fully mineralized in life (Fig. 2.A-B), the expected polyaulacorhizous basal surface of each tooth appears to have been eroded and is poorly defined. Perhaps the laminae of these young teeth had not yet fully mineralized at the time of death, *i.e.*, they consisted of soft tissue, which did not preserve (favored interpretation), or they were eroded as a consequence of a taphonomic process, (perhaps, although this would appear to be less likely given that the polyaulacorhizous roots further forward on the tooth plate are fully formed).

5. Concluding remarks

Chondrichthyan tooth abnormalities were first described in the late 1700s. ANDRE (1784) figured a jaw of extant *Galeocerdo* that had been pierced by a stingray tail spine. DELFORTRIE (1877) and WOODWARD (1888) also noted dental anomalies in fossil forms. Much more recently, CADENAT (1962) described and figured eight kinds of feeding-related dental injuries/abnormalities (Types 1-8) in extant chondrichthyans. BECKER *et al.* (2000) surveyed 200 modern lamniform and carcharhiniform sharks, concluding that chondrichthyan tooth deformities come about as a result of feeding-related injury to the dental lamina, particularly by impaction of chondrichthyan and teleost fin and tail spines. Likewise, BALBINO and ANTUNES (2007) described chondrichthyan tooth deformities that they thought were caused by damage to the dental lamina by hard foreign objects, like bone or ray spines.

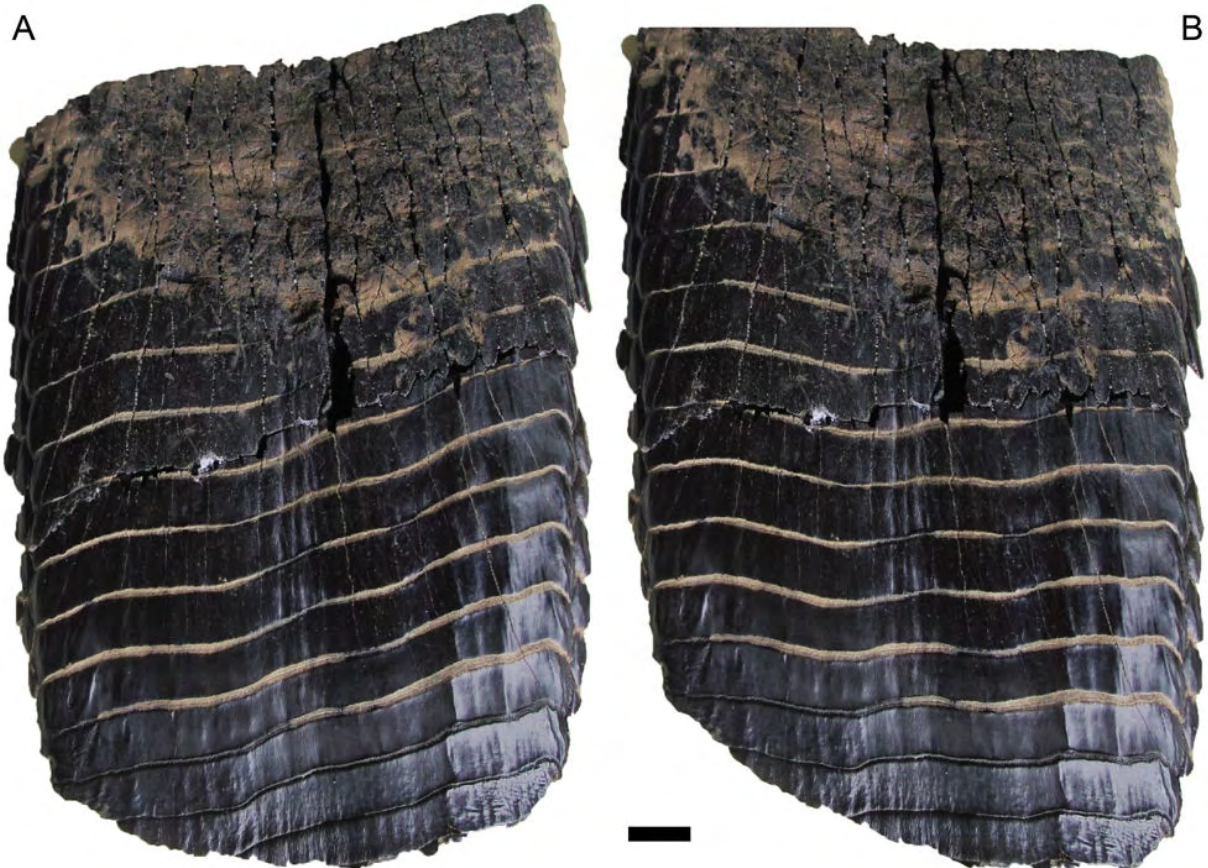


Figure 3: USNM PAL 726325 eagle ray (*Aetomylaeus* sp.) partial tooth plate seen in occlusal view. A. Tooth plate showing its natural configuration preserving the semi-circular wear pattern on its anterior margin. B. Tooth plate altered in Photoshop® to correct for the right-hand skew. Now the wear pattern is skewed towards the posterior right. Scale bar equals 10 mm.

CAPPETTA (2012, Fig. 20) also described and figured a variety of chondrichthyan tooth abnormalities, but none in rays. GUDGER (1933) described unusual dentitions in rays. In the Myliobatidae, the dental abnormalities that he described consisted almost entirely of asymmetrical differences in tooth counts, only within the genus *Myliobatis*. Three published specimens show some similarity to USNM PAL 726325. They include a specimen attributed to the extant *Aetobatus narinari* (HOVESTADT & HOVESTADT-EULER, 2013, Pl. 14, fig. 1a), the fossil "*Aetobatis*" *irregularis* (AGASSIZ, 1843) (HOVESTADT & HOVESTADT-EULER, 2013, Pl. 28, fig. 1), where the teeth are not symmetrical, and the fossil form *Myliobatis irregularis* DIXON, 1850 (HOVESTADT & HOVESTADT-EULER, 2013, Pl. 31, fig. 1). HOVESTADT and HOVESTADT-EULER (2013) reported that there is strong ontogenetic heterodonty in tooth morphology within *Aetomylaeus*. However, the skewed abnormal form of the teeth in USNM PAL 726325 is not the result of ontogenetic or sexual heterodonty, nor is it thought to be the result of the localized impaction of fin or tail spines, nor from modern or taphonomic deformation. It would be difficult to account for such a uniform taphonomic deformity given that the teeth are for the most part intact, showing no

signs of breakage. We do not know how or when in the life of this eagle ray the dental lamina became deformed. Was it an embryonic developmental irregularity/perturbation (*i.e.*, congenital), or the result of physical trauma?

GUDGER (1937), UNDERWOOD *et al.* (2015), and RASCH *et al.* (2020), all report that in sharks, skates, and rays, tooth replacement begins from the successional lamina, which is continuous with the dental lamina (GUDGER, 1937; UNDERWOOD *et al.*, 2015; RASCH *et al.*, 2020). The deformity in USNM PAL 726325 gives every indication that successive similarly deformed teeth came about as a result of a persistent anatomical deformity of the dental lamina. It is not known what caused the original deformity (*e.g.*, if the jaw cartilage beneath the dental lamina was deformed), but evidently it interfered with tooth formation from the earliest stage in growth of the tooth germ. We know of no report of an impacted hard object resulting in such a widespread deformity. From the consistency in the deformed shape of each tooth, it would appear as though the dental lamina retained this anomalous shape, at the very least throughout the time represented by the age of the tooth plate. If this interpretation is correct, the deformity was not fatal and did not significantly impair the functionality of the tooth pavement over a protracted part (or all)



of the individual's lifespan. Apparently, there are no quantitative data on the rates of tooth replacement in rays (BERKOVITZ & SHELLIS, 2017).

Although the anterior end of the tooth plate in USNM PAL 726325 is asymmetrical, the posterior end is very nearly symmetrical (Fig. 2). On a normal plate, growth is like an assembly line; one tooth or row forms and moves forward so that the next tooth (or row) can form. Presumably, in a normal dentition, the full width of each tooth would express/present very nearly the same level of mineralization. However, in USNM PAL 726325 (Fig. 2.C), the roots of the teeth are more fully mineralized/developed on the right-hand side of the dentition (*i.e.*, left-hand side of the image). In fact, in Figure 2.C, the polyaulacorhizous roots are present on the right-hand side of the fourth tooth, whereas they are not formed in the center or left-hand side of that tooth. Therefore, that part of the tooth that is further forward on the conveyor belt is more completely developed, whereas the same tooth on the left appears to be in an earlier stage of formation. Therefore, not only does the tooth plate function properly despite the abnormality, but also it develops symmetrically. One developmental program is turning out individual teeth of the proper size (length and width), although at an abnormal angle, yet the stage of development overlying it (place on the conveyor belt), working at the same time, is seemingly ignoring the tooth boundaries. What is remarkable about this deformity is that the teeth, although misshapen, appear to have been fully functional in their collective ability to crush hard prey. It is not known if the teeth in the opposing jaw were similarly deformed, but the wear pattern at the anterior end of the tooth plate appears to be bilaterally symmetrical (Figs. 2, 3.A), suggesting that occlusion between the upper and lower tooth plates was normal. To show that the existing semicircular wear pattern is symmetrical, an image of the tooth plate was altered in Photoshop® so as to "correct" for the deformity (Fig. 3.B). Once this was done, the originally symmetrical wear facet became skewed posteriorly towards the right side of the plate. The area of wear (occupying about one-third of the plate as preserved and as measured down the center) is in keeping with other *Aetomylaeus* sp. tooth plates. Despite the normal, symmetrical wear pattern, the leading-edge tooth loss was along the skewed tooth boundary. It is not possible to determine if the current anterior end of the tooth plate represents the pre- or postmortem condition, and whether the plate is complete anteriorly. Somewhat unexpectedly, the medial (symphyseal) teeth decrease in width by 4 mm from front (older teeth) to back (younger teeth). We would have expected these teeth to increase in width from front to back.

This anomalous tooth plate would appear to confirm that there is a level of tooth deformity (*i.e.*, accommodation/adaptability/plasticity in the development of, and overall tooth shape) below which each tooth and resulting tooth plate remains functional. In other words, individual teeth do not have to conform to a precise shape for the tooth plate to remain adequately functional, provided that at least all the teeth in the tooth plate are similarly mildly deformed. The specimen described here would suggest that deformed tooth primordia in *Aetomylaeus* can assume a slightly modified/anomalous shape and still develop into, by all appearances, a functionally normal tooth plate.

A classification scheme was created by CADENAT (1962) to distinguish between different types of dental anomalies that can occur when a foreign body becomes lodged in the jaw due to feeding. GODFREY *et al.* (2021) came to a similar conclusion to account for a linear groove lesion in a Miocene *Aetobatus arcuatus* lower dental plate also found along Calvert Cliffs, Maryland. In the case reported here, however, it is unlikely that a foreign body embedded in the tessellated cartilage adjacent to the successional lamina could have caused this kind of persistent deformity to the whole medial tooth within the successional plate. Rather it would seem as though much or all of the dental lamina was evenly deformed, resulting in consistently deformed, but seemingly adequately functional crushing medial teeth. We do not know how deformed teeth could be, and yet remain functional. Presumably, at some point beyond the degree of tooth deformity presented by USNM PAL 726325, a deformed dental lamina would be so great as to preclude the formation of functional teeth, and the functionality of the dentition would simply fail and the animal would die. It is also noteworthy that the paired lateral teeth exhibit no evidence of strong deformity and their positional relationship to the medial teeth is apparently normal.

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