Multiple Tooth-Rowed Parareptile From the Early Permian of Oklahoma

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The Dolese Limestone Quarry near Richards Spur, Oklahoma includes an elaborate system of caves which have been infilled with early Permian fossil rich sediments. In operation for more than a century, the quarry yielded vast numbers of disarticulated skeletal elements of the most diverse assemblage of fully terrestrial tetrapods from the Paleozoic. Excavations carried out in this century are distinct in producing large numbers of articulated and semiarticulated skeletons, including numerous new taxa. Dolese is therefore unique among early Permian localities in being home to a diverse assemblage of small parareptiles, including two species of Delorhynchus. Here we describe a new species of acleistorhinid, characterized by the presence of multiple tooth rows on the dentary, that can be identified with confidence as a third new species of Delorhynchus. The multiple tooth rowed condition is deemed not to be a pathological condition, and appears to have formed in the same manner as in the captorhinid eureptile Captorhinus aguti through uneven growth of the tooth-bearing element.

Keywords: acleistorhinid parareptile, dental battery, early permian, Oklahoma, new taxon

INTRODUCTION

The Richards Spur locality in Oklahoma, also known as the Dolese Brothers limestone quarry, is a highly fossiliferous site containing an unparalleled variety of early Permian tetrapods (Modesto, 1999; MacDougall and Reisz, 2012; MacDougall et al., 2016). Investigation of the site's geology and taphonomy has revealed an extensive karst system within Ordovician strata, filled with clay and mudstone deposited 289 to 286 million year ago (Sullivan et al., 2000; Woodhead et al., 2010; MacDougall et al., 2017). The entirety of fossil material collected from Richards Spur originates from these fissures, with varying degrees of articulation and wear present (MacDougall et al., 2017). Of the numerous tetrapod taxa found in Richards Spur, eight are assigned to Parareptilia (Vaughn, 1958; Fox, 1962; Reisz et al., 2002; Tsuji et al., 2010; MacDougall and Reisz, 2012; MacDougall and Reisz, 2014; Reisz et al., 2014; MacDougall et al., 2016).

Parareptilia comprises one of the major amniote clades of the Permian, possessing a wide variety of distinct morphologies and distributed globally (Debraga and Reisz, 1996; MacDougall et al., 2019). This clade of amniotes originated as small-bodied carnivores, but experienced significant increases in diversity throughout the Permian (Reisz et al., 2015; MacDougall et al., 2019). Relative completeness of some parareptilian remains has enabled identification of diverse morphologies including small
carnivores, aquatic filter-feeders, and megaherbivores (Lee, 1999; Reisz et al., 2002; Modesto, 2006; Cisneros, 2008; Tsuji et al., 2012; MacDougall and Reisz, 2014; LeBlanc and Reisz, 2015; Verrière et al., 2016). Parareptiles were also diverse in body size, with skulls between 2 and 45 cm in length (Lee, 1999; Berman et al., 2000). In the Early Permian, parareptiles were relatively small with skulls at or under 5 cm in length (Modesto et al., 2009). The frequency of parareptilian remains in Richards Spur is unusual given their sparse occurrence in most other deposits of similar age (Cope, 1878; Tsuji et al., 2010). Many parareptiles found within Richards Spur belonged to the small-bodied Acleistorhinidae (Vaughn, 1958; Fox, 1962; Daly, 1969; Modesto, 1999; Tsuji et al., 2012; Reisz et al., 2014; MacDougall et al., 2016). While the majority of acleistorhinid species have been found within Oklahoma, remains have also been found in Nova Scotia, Ohio and even in Brazil (Mann et al., 2019; Cisneros et al., 2020b). Acleistorhinids can be traced back as far as the late Carboniferous, and were most likely insectivorous in general based upon tooth morphology and even associated remains of insect cuticle (Modesto et al., 2009; Mann et al., 2019). The occurrence of numerous acleistorhinid species in a relatively small geographical area has led to the hypothesis that it was a hotspot for parareptile diversification (MacDougall et al., 2016).

One acleistorhinid identified from Richards Spur is Delorhynchus, which was first described as a “pelycosaur” based on an isolated maxilla (Fox, 1962). Reclassification of the “protorothyridid” Colobomycter pholet as an acleistorhinid also tentatively identified D. priscus as a sister taxon to C. pholet and Acleistorhinus ptetoticus (Modesto, 1999). Evidence of an insect-based diet was supported by small, sharp marginal dentition and, more remarkably, the discovery of arthropod cuticle in the oral region of cranial material that has since been assigned to Delorhynchus (Modesto et al., 2009; Reisz et al., 2014). The discovery of a partial skeleton and skull resulted in the subsequent description of a new species of Delorhynchus, D. cifelli, and placement of Delorhynchus within the Acleistorhinidae (Reisz et al., 2014). Further studies have resulted in a potential ontogenetic sequence of jugal morphology and implications for closure of the temporal fenestra, as well as evidence of multiple denticulate coronoids previously unseen in reptiles (Haridy et al., 2016, Haridy et al., 2018). The “microsaur” Bolorpeton carrolli from Richards Spur, described on the basis of a mandibular fragment, was also reassigned to D. cifelli (Anderson and Reisz, 2003; Haridy et al., 2018). In this paper, we report the discovery of mandibular and cranial material that in most aspects closely resembles previously described specimens of D. cifelli. However, in contrast to other referred specimens of Delorhynchus, a double row of dentary teeth is present. The addition of this novel taxon further contributes to the considerable parareptile diversity present at Richards Spur, as well as a novel occurrence of multiple tooth rows within the Parareptilia.

SYSTEMATIC PALEONTOLOGY

PARAREPTILIA Olson, 1947.

PROCOLOPHONOMORPHA Romer, 1964.

ANKYRAMORPHA deBraga and Reisz, 1996.

DELRHYNCHUS Fox, 1962.

DELRHYNCHUS MULTIDENTATUS, sp. nov. (Figure 1).

Holotype—ROMVP 87042—fragmentary skull.

Diagnosis—Acleistorhinid parareptile characterized by the presence of distinct, separate rows of teeth on the dentary, and an enlarged labial foramen on the dentary. Similar to Delorhynchus cifelli in the presence of distinct tuberculous ornamentation of the skull roof elements. Differs from D. cifelli in the more bulbous shape of the dentary teeth, with little or no evidence of recurvature.

Locality and Horizon—Dolese Brothers Quarry near Richards Spur, Oklahoma, United States Lower Permian/ Cisuralian (289 Ma).

Etymology—Specific epithet refers to the diagnostic feature of this taxon.

METHODS

Non-destructive, thermal-neutron microtomographic measurement of specimen (ROMVP 87042) was performed using the DINGO thermal neutron radiography/tomography/imaging station, located at the 20 MW Open-Pool Australian Lightwater (OPAL) reactor housed at the Australian Nuclear Science and Technology Organisation (ANSTO), Lucas Heights, New South Wales, Australia.

For this study, DINGO was equipped with an Iris 15 sCMOS camera (16-bit, 5,056 × 2,960 pixels) coupled with a Makro Planar 100 mm Carl Zeiss lens and a 20 µm thick terbium-doped Gadox scintillator screen (Gd2O2S:Tb, RC Tritec AG) to yield a pixel size of 13.7 × 13.7 µm and field of view was of 40.6 × 69.3 mm². DINGO was operated in high-flux mode, with a collimation ratio (L/D) of 500 was used, where L is the neutron aperture-to-sample length and D is the neutron aperture diameter, supplying a flux at sample of 4.75 × 10⁷n cm-²s⁻¹ (Garbe et al., 2015). The tomographic scan consisted of a total of 1,440 equally-spaced angle shadow-radiographs obtained every 0.125° as the sample was rotated 180° about its vertical axis, which was positioned 15 mm from the detector face. Both dark (closed shutter) and beam profile (open shutter) images were obtained for calibration before initiating shadow-radiograph acquisition. To reduce anomalous noise, a total of three individual radiographs with an exposure length of 12.5 s were acquired at each angle (Mays et al., 2017). Total scan time was 16.5 h.

Neutron activation of the specimen was measured by surface contact using an appropriate hand-held dosimeter, 35 min upon completion of the scan, at 4 days, and 2 weeks post-scan. The recordings were 13, 1 and 0 µSv/h, respectively. The specimen was issued a radiation clearance certificate and cleared for return to the authors shortly thereafter, with no detectable counts per second above background recorded by the health physics surveyor.

The individual radiographs were summed in post-acquisition processing using the Grouped ZProjector function, and anomalous white-spots removed using a threshold filter in
ImageJ v.1.51 h. Normalisation and tomographic reconstruction of the 16-bit raw data were performed using Octopus Reconstruction v.8.8 (Inside Matters NV), yielding virtual slices perpendicular to the rotation axis. Prior to segmentation, the specimen scan was processed in ImageJ. Thorough segmentation of the specimen was performed on Avizo Lite registered to R. R. Reisz, and the model was compared to other specimens of *D. cifelli* specimens OMNH 73362 and OMNH 73363 for identification purposes. Photographs of the specimen were taken using a Leica microscope and associated software. Figures were assembled using Adobe Photoshop Elements 8.0.

**DESCRIPTION**

This holotype specimen is composed of a partial left mandibular fragment, two dentigerous palatal elements, two cranial elements and other small cranial fragments (see Figures 1–4 for visualization). The mandibular fragment belongs to the left side of the cranium and possesses a readily identifiable dentary, coronoid and splenial. Fragmentation of the posterolingual section results in numerous mandibular fragments which cannot be confidently identified. Surrounding the mandible fragment are a mostly complete jugal and squamosal, both from the left side of the skull. Ventral to the jugal and squamosal are small fragments of cranial material belonging to the ectopterygoid and pterygoid, as well as a fragment of the posterior splenial. The close association of these elements and the known breakages suggest that this specimen represents the remnants of a single skull. It is likely that the specimen was discovered as a fragment, and was a complete or near-complete skull damaged during the excavation process normally carried out by the limestone quarrying operations.

The dentary fragment in this specimen comprises the majority of the articulated mandibular fragment and possesses a dental
pattern not seen in previous Delorhynchus material. While other specimens of D. cifelli possess a single row of dentary teeth, this specimen instead possesses two rows, hereafter referred to as lingual and labial. A total of twenty-five sockets are present within the preserved fragment, with thirteen sockets assigned to the lingual row and twelve in the labial row. The anterior region of the dentary possesses two shallow labial foramina as well as a much wider and deeper foramen which entirely passes through the dentary fragment, with thirteen sockets assigned to the lingual row and twelve in the labial row. The anterior region of the dentary possesses two shallow labial foramina as well as a much wider and deeper foramen which entirely passes through the dentary fragment, with thirteen sockets assigned to the lingual row and twelve in the labial row. 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smooth texture and possesses two anterior projections that join onto the dentary (Haridy et al., 2018). In this specimen, the splenial is only in articulation with the anterior half of the mandible. Towards the posterior, the splenial has been broken off and is found in association with the anteroventral region of the specimen. The anterior fragment sutures onto the dentary both dorsally and ventrally, as well as the coronoid dorsally. The disarticulated posterior splenial fragment would possess similar contacts with the dentary.

Angular elements in specimens of Delorhynchus cifelli are dorsally curved, and extend from the inside of the anterior mandible out to form part of the posterolabial surface of the mandible (Reisz et al., 2014; Haridy et al., 2018). In full articulation, the angular contacts the dentary and splenial anteriorly, the surangular dorsally and the articular posteriorly (Haridy et al., 2018). For this specimen, the angular has been disarticulated, and is present within the posteroventral region of the mandibular fragment. Identification of the angular is based on curvature, although much of the element has been fragmented and is missing.

The surangular has been described as a complex element that contributes to multiple characteristics of the lower jaw of Delorhynchus cifelli (Haridy et al., 2018). These features include a posterior sheet which overlies the articular labially, part of the labial component of the coronoid process, and the internal wall of the adductor fossa (Reisz et al., 2014; Haridy et al., 2018). In addition, a thin anterior process underlies the dentary, which terminates at the anterior process of the posterior coronoid (Haridy et al., 2018). A small portion of the surangular element has been identified in the posteroventral region in the holotype of D. multidentatus, and based upon the narrow sheetlike appearance it likely belongs to the anterior surangular process. In Delorhynchus cifelli, the prearticular is wedged between the splenial and the posterior coronoid process, and borders the splenial, angular and intermandibularis foramen caudalis ventrally (Haridy et al., 2018). This lingual element is thin and elongated, and also possesses a well-defined ridge that forms a slanted shelf in the posterior prearticular (Haridy et al., 2018). As is the case with the angular, the prearticular has been disarticulated and fragmented, and is framed within the articulated dentary and splenial. Identification of the prearticular was based on its thinness and sharp ridge.

In this specimen, the left jugal has suffered slight anterior breakage, but is otherwise mostly complete as shown in Figure 7.

**FIGURE 3 |** Delorhynchus multidentatus, sp. nov., ROMVP 87042. (A) labial, (B) lingual and (C) occlusal views of partial mandible, (D) occlusal view of partial mandible with numbering of tooth positions Scale bar = 5 mm. Abbreviations: A1–A13, labial tooth positions 1–12, an, angular; cr, coronoid; d, dentary; I1–I12, lingual tooth positions 1–12; pre, prearticular; sp, splenial; sur, surangular.
This skull roof element is tetraradial, with shallow furrows and sculpted dimples. A deep posterodorsal emargination is present that would form the anterior half of the ventral border and the anterior border of the temporal fenestra. The suborbital bar
terminates in a break, immediately anterior to an incomplete wedge-shaped alary process that extends medially. Comparison with a previously presented ontogenetic sequence of *Delorhynchus cifelli*, as well as a skull as shown in Figure 8 indicate that the jugal morphology of *D. multidentatus* most closely resembled the most mature specimens of *D. cifelli* (Haridy et al., 2016). However, the jugal of *D. multidentatus* was significantly smaller, which reflects an adult specimen of comparatively smaller size. It is largely in position relative to the mandibular fragment, but is rotated such that it forms the most dorsal region of the specimen.

The left squamosal (see Figure 9 for visualization) is a tall element and possesses a rosette-shaped pattern of large tuberosities on the lateral surface that would cover other elements of the skull roof. In addition, the posterior surface is smooth and concave, as in previously described specimens of *Delorhynchus cifelli*. This specimen also possesses a shelf on the dorsal region, which would suture onto the supratemporal. Towards the posteroventral region, a small groove is present which would suture onto the quadratojugal.

Within the palate of *Delorhynchus cifelli*, the ectopterygoid makes a minor contribution to palatal dentition, nestled among the palatine, pterygoid, maxilla, and jugal (Reisz et al., 2014). Only a small number of denticles are present on the ventral surface, which is dominated by a large, but very shallow concavity (Reisz et al., 2014). While this element is predominantly thin, it also has thickened lateral and posterior margins (Reisz et al., 2014). The tentatively identified ectopterygoid in this specimen is only partial, and its medial surface has been broken. The ventral surface of the ectopterygoid can be clearly identified based on a small cluster of palatal teeth that are partially disarticulated, as
well as two small denticles that are fully articulated. A thickened process present on the ectopterygoid would form a lateral contact with the medial process of the jugal.

In contrast to the ectopterygoid, the pterygoid makes a much larger contribution to the palatal dentition of Delorhynchus cifelli (Reisz et al., 2014). This element is highly complex, and can be subdivided into an anterior process, an angular transverse process and a posterior quadrate ramus (Reisz et al., 2014). In the holotype of D. multidentatus, the tentatively identified left pterygoid is only present as a section of the transverse process, based on the sharply concave groove which is also present in D. cifelli. Only one denticle is present towards the posterior region, and the anterior region of the preserved element is highly fragmented.

**DISCUSSION**

This specimen can be readily identified as a distinct new taxon. This conclusion is based on the unique combination of a wide alveolar shelf on the dentary, multiple rows of dentary teeth, small size and ornamentation of the dentary. With the description of Delorhynchus multidentatus, there are now three members of the Delorhynchus genus, all located entirely within the Richards Spur cave system (Fox, 1962; Reisz et al., 2014). With the associated remains of insect cuticle with D. cifelli and comparable dentition in each species, all members of Delorhynchus were therefore small-bodied and insectivorous (Modesto et al., 2009). With the discovery of D. multidentatus, there are now nine distinct species of parareptiles within five genera from the Richards Spur locality (Vaughn, 1958; Fox, 1962; Reisz et al., 2002, 2014; Tsuji et al., 2010; MacDougall and Reisz, 2012; MacDougall et al., 2016). It must be noted that comparison with D. priscus is not possible, given that a single maxilla was assigned as the holotype of D. priscus and no maxilla has been preserved with the holotype of D. multidentatus (Fox, 1962). The known skull and mandibular elements are similar to those known in D. cifelli, but only a single row of dentary teeth are present in that species (Modesto et al., 2009; Reisz et al., 2014; Hardy et al., 2018). In addition, each tooth is also proportionately larger in D. cifelli and occupies a greater portion of the dentary than in D. multidentatus, as would be expected when a single tooth row is present (Hardy et al., 2018). The dentary teeth of D. multidentatus are not sharp and show no recurvature unlike the known insectivore D. cifelli (Modesto et al., 2009). However, the broad similarities between these two taxa as well as the diminutive size of D. multidentatus means that this new acleistorhinid was likely to have pursued similar prey. The presence of low tuberosities on the squamosal, as well as shallow dimples and furrows on the jugal, help further characterize this specimen as a member of the Delorhynchus genus. In this holotype specimen, the jugal can be readily compared to material from D. cifelli, and its morphology matches the most mature specimens of D. cifelli despite the comparatively smaller size of this skull roof element (Hardy et al., 2016). Inspection of the rows of teeth demonstrates that the lingual row of teeth has partially eroded the labial row of teeth, which implies that the lingual row developed after the labial row. Based upon this observation, and the size disparity between teeth in each row, it is likely that rows of teeth developed on the lingual side, eroding the older row as they grew, but shifted labially to a degree sufficient to form multiple rows of teeth. D. multidentatus additionally possesses a wider alveolar shelf than D. cifelli, as shown in Figure 6. This feature acts as secondary support for the proposed labial drift of teeth, and is shared with some specimens of the multiple tooth-rowed eureptile Captorhinus aguti (LeBlanc and Reisz, 2015). In C. aguti, histology of the dentary reveals the presence of labial drift via asymmetric dentary growth and a resulting odontogenic region for tooth development and replacement (LeBlanc and Reisz, 2015). While the CT resolution for D. multidentatus is insufficient for determining patterns of vascularization, the enlarged alveolar shelf suggests that, as in C. aguti, D. multidentatus developed its teeth in a lingual odontogenic region. The tooth development in D. multidentatus appear to
be similar to that of *C. aguti* in that rows of teeth in both species originated lingually and were migrated outwards towards the labial side by differential growth of the dentary bone (LeBlanc and Reisz, 2015). In contrast to the diagonal, mesial to distal tooth row development within the posterior dentary of *C. aguti*, the multiple tooth rows in *D. multidentatus* grew parallel to the dentary throughout its length (LeBlanc and Reisz, 2015). The orientation of tooth rows in *C. aguti* results in a grinding surface suitable for this taxon’s omnivorous diet (Holton et al., 1997).

Multiple rows of dentary teeth have historically been an unusual condition in early Permian tetrapods, with one other occurrence in the Parareptilia, two independent developments within the captorhinids and another occurrence in a “microsaur” (Dodick and Modesto, 1995; Gee et al., 2020). The middle Triassic procolophonid parareptile *Theledectes perforatus* also possessed multiple rows of marginal dentition, although given the spatial, temporal and phylogenetic separation from *Dolorhynchus multidentatus* this is regarded as a convergent trait (Gow, 1977; Modesto and Damiani, 2003). In the genus *Captorhinus*, *C. aguti* possessed multiple dentary tooth rows, while *C. laticeps*, *C. magnus*, and *C. kierani* were single tooth-rowed (Williston, 1909; Fox and Bowman, 1966; Kissel et al., 2002; DeBraga et al., 2019). Other small captorhinids from the early Permian with multiple tooth rows include *Baeotherates forstilensis* and the genus *Captorhinikos* (May and Cifelli, 1998; Modesto et al., 2014; Leblanc et al., 2015; Cisneros et al., 2020a). In *C. aguti* and *Captorhinikos*, as well as other multiple tooth-rowed captorhinids from the Middle and Upper Permian, the tooth rows extend parasagitally with younger lingual and older labial teeth (Fox and Bowman, 1966; Modesto et al., 2014, 2018). *B. forstilensis* differs from other captorhinids in that it possesses only two rows of dentary teeth aligned diagonally to the dentary, but it is not known whether this feature developed independently of other multiple-rowed captorhinids due to limited material (May and Cifelli, 1998; DeBraga et al., 2019). The presence of dual tooth rows has also been documented within early Permian non-amniote tetrapods, such as in the gymnarthrid “microsaur” *Euryodus dalyae* which possesses a partial double tooth row at the posterior edge of the dentary (Gee et al., 2020).

A recent study on extant phrynosomatid lizards *Uta stansburiana* and *Petroaurus mearnsi*, which are normally single tooth-rowed taxa excluding specimens within said study, hypothesizes that developmental irregularities in odontogenic gene expression may result in multiple tooth rows (Scarpetta and Bell, 2020). In these cases, the specimens appear to have experienced crowding of tooth positions resulting in multiple tooth rows on an unexpanded alveolar shelf (Scarpetta and Bell, 2020). These recent findings raise the possibility of single tooth-rowed taxa being designated as possessing multiple tooth rows as a result of developmental abnormalities. Due to the specific development of multiple tooth rows in this new aceleistorhinid taxon, as well as other features such as reduced skull size, we consider this hypothesis unlikely for *Dolorhynchus multidentatus* and believe it to be a new taxon rather than a specimen of *D. cifelli* with unusual tooth development. In *D. multidentatus*, the mandible contains morphologically distinct teeth with a widened alveolar shelf. In particular, the alveolar shelf is significant in that it provides room for additional tooth positions that would otherwise result in the anomalous crowding as shown in Scarpetta and Bell (2020). In contrast to the more distinct tooth rows seen in other multiple tooth-rowed taxa such as the moradosaurine *Captorhinikos valensis*, CT data show that some replacement teeth in this specimen have eroded into the pulp cavities of older teeth (see Figure 4) (Modesto et al., 2014), but the older teeth appear to remain functional. In *Captorhinus aguti*, the wide alveolar shelf present on the dentary is the product of asymmetric growth and apparently results in the labial shift of tooth rows, which is also hypothesized for *D. multidentatus* based on examination of tooth-bearing material (LeBlanc and Reisz, 2015). In *Euryodus dalyae*, the presence of multiple tooth rows differs significantly from the aforementioned taxa, as only the two posteriormost tooth positions occur in multiple rows (Gee et al., 2020). While the teeth produced in the multiple tooth rows in *Euryodus* are small, the alveolar shelf present in this specimen is widened, likely the result of the large coronoid process posterior to it (Gee et al., 2020). This coronoid process may have labially shifted the older, smaller teeth during ontogeny, away from the dental lamina and the teeth being produced there, leading to two functional teeth in one position. Given the proposed labial drift of *D. multidentatus* and minor overlap of teeth resulting in partial erosion of old teeth, it is possible that the condition of this aceleistorhinid represents an intermediate form between what is demonstrated by Scarpetta and Bell (2020) and other multiple tooth-rowed taxa such as moradosaurines. Nevertheless, it is likely that the development of multiple tooth rows among aceleistorhinids was part of the hypothesized radiation of parareptiles within Richards Spur, resulting in the retention of a second tooth row in *D. multidentatus* (MacDougall et al., 2016; Scarpetta and Bell, 2020) It is clear that early Permian tetrapods with multiple tooth rows are rare in the fossil record. *Theledectes perforatus*, *Captorhinus aguti*, *Euryodus dalyae* and moradosaurines such as *Captorhinikos* each developed dental batteries independently of one another (Fox and Bowman, 1966; Modesto and Damiani, 2003; Modesto et al., 2014; Gee et al., 2020). In each case, there is an increase in complexity of dentition without corresponding changes in dentition shape, in contrast to the change in dentition shape seen in *Diadectes* for the purposes of oral processing (Cope, 1880). The discovery of *D. multidentatus* not only contributes to the diversity of aceleistorhinids within the early Permian of Oklahoma, but also documents the first case of multiple tooth rows within the Aceleistorhinidae.

**DATA AVAILABILITY STATEMENT**

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.
AUTHOR CONTRIBUTIONS

DR analysed the data, wrote first draft of the article, and produced the CT figures. JB performed the neutron analysis and contributed the article. RR designed the project, contributed specimens, and contributed to the article. DS discovered specimen, prepared and contributed photographs. All authors approved the submission of this article.

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