ANNALS OF CARNEGIE MUSEUM

VOL. 67, NUMBER 2, PP. 181–196 12 MAY 1998

TAXONOMIC STATUS OF THE EARLY PERMIAN *HELODECTES PARIDENS* COPE (DIADECTIDAE) WITH DISCUSSION OF OCCLUSION OF DIADECTID MARGINAL DENTITIONS

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ABSTRACT

Helodectes paridens Cope (1880) is a problematic Early Permian taxon from Texas that has been considered variously as a diadectid or captorhinid, or simply indeterminate. It was based on a poorly preserved jaw and adjoining elements of the left side of a small skull that was believed to possess a double row of marginal teeth. Thorough preparation of the holotype reveals that one row represents a normal complement of rooted premaxillary and maxillary teeth and the other a row of crowns derived from the opposing teeth of the absent dentary. There are no detectable differences from the commonly encountered *Diadectes* of the same age, and *Helodectes* should be regarded as a junior synonym of that genus. As the holotype of *H. paridens* exhibits no features on which to base specific identity, it is referred to as *Diadectes* sp. The same interpretation undoubtedly applies to the double row of premaxillary–maxillary marginal teeth in the lost and only known specimen of the equally small holotype of *H. isaaci* Cope (1880) from the same locality as *H. paridens*. A second example of *Helodectes*-like dental preservation is described in the opposing upper and lower jaw elements in a very small *Diadectes* specimen from the Early Permian of Texas.

The double-toothed row preservation of the marginal teeth in these specimens prompts discussion of aspects of the occlusion of the cheek teeth in *Diadectes* and those in the closely related Late Pennsylvanian *Desmatodon*. It is speculated that, in addition to occlusion between the upper and lower cheek teeth, mastication also occurred through contact between the maxillary cheek teeth and the inner surface of the parapet of the dentary, and between the cheek teeth of the dentary and the ventral surface of the secondary palatal shelf of the palatine. Changes in the pattern of attrition indicate that with increased molarization the occlusion between the upper and lower cheek teeth shifted from a strictly side-to-side contact in extremely small juveniles to a strictly dorsoventral, vertical-alignment contact between the upper surfaces of the crowns in adults. In the adult pattern of occlusion the upper and lower cheek-tooth series were only partially aligned dorsoventrally, and it is assumed that the labial margin of the upper series and the lingual margin of the lower series occluded with the inner surface of the dentary parapet and the ventral surface of the secondary palatal shelf of the palatine, respectively. These changes in the molarization and occlusion from extremely small juveniles to adults may have been accompanied by a shift in diet.

KEY WORDS: Diadectidae (*Diadectes*), *Helodectes*, dentition, Early Permian

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Submitted 3 April 1997.

INTRODUCTION

Olson's (1947) study of the family Diadectidae was initiated with the aim of 1) better understanding the Cotylosauria, then considered by most to include all the primitive reptiles lacking temporal openings and comprising the Diadectomorpha, Captorhinomorpha, and Seymouriamorpha; and 2) a revision of the classification of the Reptilia, now considered as a paraphyletic grouping. The diadectomorph family Diadectidae was considered by him as occupying a central position to these two endeavors, because it is the family on which Cotylosauria was founded and because of the availability of specimens of its member genera, particularly the type genus *Diadectes*, that permitted detailed anatomical study. Upon examination of most of the existing diadectid materials collected from the Late Pennsylvanian and Early Permian of North America, Olson (1947) concluded that of the then 11 recognized genera only *Diadectes* Cope, 1878, *Desmatodon* Case, 1908, and *Diasparactus* Case, 1910, are valid taxa. Subsequent studies of new and more complete specimens of the poorly known *Desmatodon* have strongly reaffirmed the validity of this taxon (Vaughn, 1969, 1972; Berman and Sumida, 1995). Seven of the diadectid genera (*Empedocles* Cope, 1878, *Nothodon* Marsh, 1878, *Chilonyx* Cope, 1883, *Empedias* Cope, 1883, *Bolbodon* Cope, 1896, *Diadectoides* Case, 1911, and *Animasaurus* Case and Williston, 1912) were reevaluated by Olson (1947) as synonymous with *Diadectes*. He concluded that the specimens on which these genera were based either exhibited no features that could be used to differentiate them from *Diadectes* or exhibited features which are highly variable with age, such as thickness and rugosity of cranial bones or proportional differences in skeletal elements, and therefore could not be considered to be of generic, or even specific, significance.

The remaining genus to be considered and the subject of this report is *Helodectes*, which was originally described and referred to the Diadectidae by Cope (1880). Cope (1880:48–49) described *Helodectes* as represented by two species, each based on a single specimen of jaw fragment with teeth and collected presumably from the same Early Permian, Wichita Group, site in Texas by Jacob Boll between 1878 and 1880 (Romer, 1958). The specimen on which was founded the first named species, *H. paridens*, was described by Cope as a left maxilla and probable adjoining premaxilla (AMNH 4346). The jaw fragment was very poorly preserved and encrusted with a very incalcitrant, oxidized iron matrix. Most unusual and forming the basis of Cope's (1880) generic diagnosis was the presence of both an inner and outer row of marginal teeth. The second species of *Helodectes* described by Cope, *H. isaaci*, was based on a probable fragment of maxilla also possessing a double row of teeth (catalogue number not given) and exhibiting the same poor quality of preservation. According to Case (1911), the holotype and only known specimen of *H. isaaci* is lost and no specimen can be identified from Cope's description. The two *Helodectes* species were distinguished from one another by the number, relative sizes, and arrangements of the teeth. Cope (1880) noted that occurring with the type specimens of both species of *Helodectes* were diadectid skeletal fragments that could belong to either of them or even to a small specimen of *Empedocles*, whose teeth were included in the same lot. These materials were not described, however, because of the uncertainty of association. Case (1911:48) believed it was very doubtful that additional specimens of *Helodectes* could be identified with confidence because of the poor quality of the holotypic material. Continuing, he remarked that the ''numerous teeth in the fragment of the jaw indicate a member of the suborder Pareiasauria, but that the fragment and the roots of the teeth indicate an animal much larger than any well-known member of the suborder.'' For these reasons he retained the genus provisionally as a captorhinid. In Olson's (1947) opinion, however, the unassigned skeletal fragments found with the holotype of *H. paridens* are so poorly preserved that only some of the postcranial fragments can be very doubtfully referred to Diadectidae. He, therefore, concluded that the jaw fragment of *H. paridens* does not belong to this group, and, although some of the associated postcranial fragments are diadectid, the genus must be rejected as indeterminate.

Preparation of the holotype of *Helodectes paridens* reveals that it possesses only a single row of rooted, premaxillary–maxillary teeth lacking their crowns. The second row of teeth observed by Cope (1880) consists of the crowns of the dentary dentition of the opposing lower jaw that has been lost due to weathering. Peter P. Vaughn of the University of California, Los Angeles, realized the true nature and origin of the dentition of *Helodectes* as early as the mid-1960s. One of us (DSB), while a graduate student of Vaughn, recalls having been told by him the explanation for the double row of teeth in *Helodectes*. His evidence was almost certainly based initially on an at-hand collection of undescribed jaw and postcranial elements of several extremely small individuals of *Diadectes* from the Early Permian of Texas (collectively catalogued as MCZ 2780). Included was a set of upper and lower jaw elements that not only exhibits the identical, double-toothed row condition seen in the holotype of *H. paridens*, but when rejoined in their original, preserved position also reveals clearly the origin of the deceptive appearance of its dentition. He later confirmed his suspicion by examining the holotype of *H. paridens*. It was not until the loan of the MCZ 2780 material was transferred to the Carnegie Museum of Natural History that the authors became aware of the *Helodectes*-like set of jaws and realized its implications. Careful examination of the holotype of *H. paridens* not only resolves the riddle of its dentition, but also provides indisputable evidence that it should be assigned to Diadectidae as *Diadectes*, although a species assignment cannot be made safely. Presumably the same conclusions would apply to the missing holotype of *H. isaaci*.

The double-toothed row preservation has prompted a reconsideration of the function of the secondary palatal shelf of the palatine and the parapet of the dentary as providing masticatory surfaces for the lower and upper cheek teeth, repectively, in *Diadectes* and the closely related Late Pennsylvanian *Desmatodon*. In addition, pronounced changes in the molarization and occlusion of their cheek teeth from extremely small juveniles to adults may have been accompanied by a shift in diet.

The following abbreviations are used throughout the text to refer to repositories of specimens: AMNH, American Museum of Natural History, New York, New York; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

DESCRIPTION OF *HELODECTES PARIDENS*, HOLOTYPE, AMNH 4346

The holotype and only known specimen of *Helodectes paridens*, AMNH 4346, consists not only of the articulated left premaxilla and maxilla, as originally described by Cope (1880), but also portions of the adjoining lacrimal, jugal, palatine,

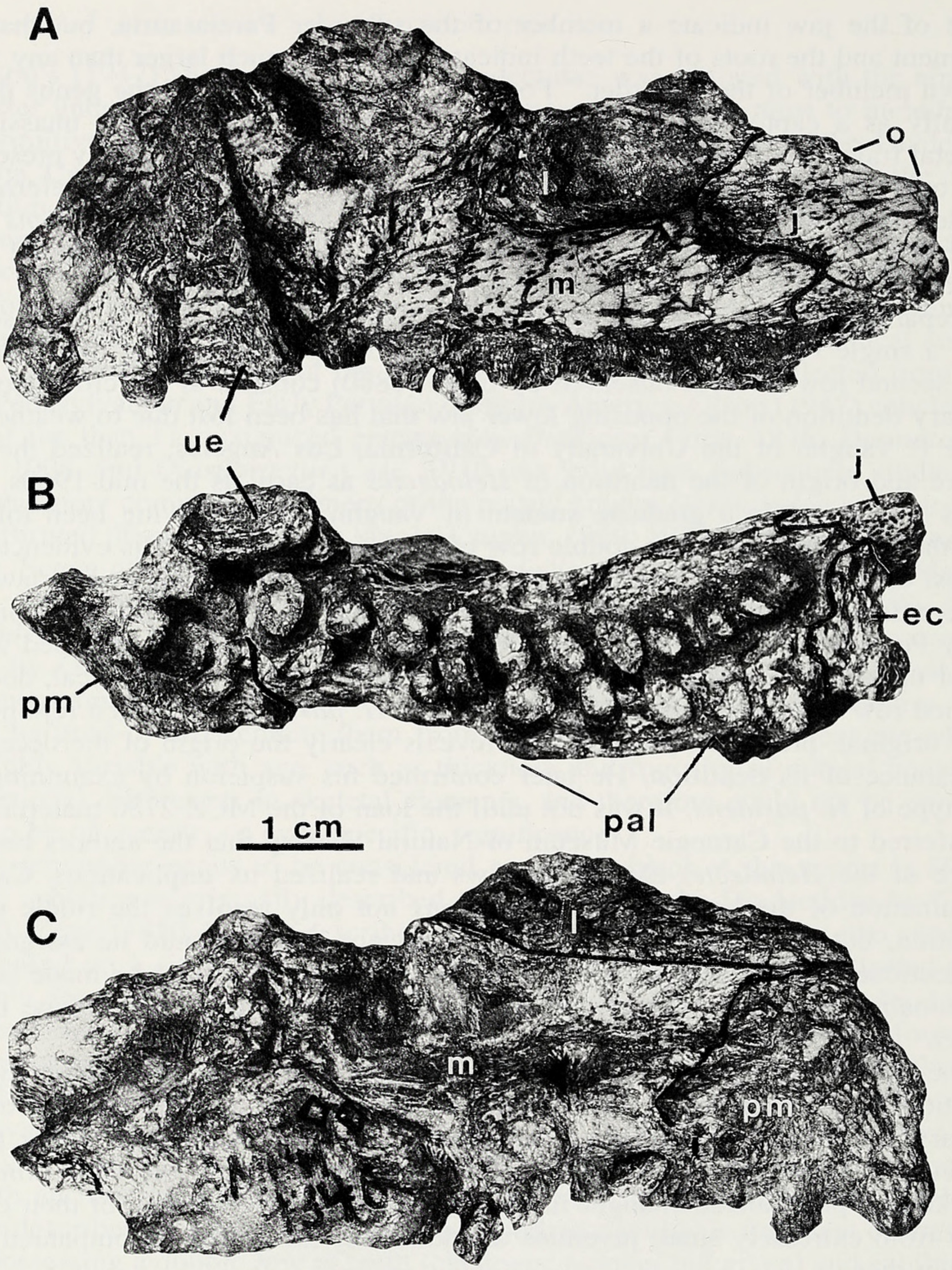

Fig. 1.—*Diadectes* sp. (AMNH 4346), holotype of *Helodectes paridens*, consisting of upper left jaw and portions of adjoining elements. A, lateral (anterior to left); B, occlusal; and C, medial (anterior to right) views. Abbreviations: ec, ectoptyergoid; j, jugal; l, lacrimal; m, maxilla; o, orbital rim; pal, secondary palatal shelf of the palatine; pm, premaxilla; ue, unidentified element.

and ectopterygoid (Fig. 1, 2). The holotype is mediolaterally crushed dorsal to the alveolar shelf, and a large, unidentified fragment of bone adheres to its lateral surface at the premaxillary–maxillary union. The premaxilla lacks the dorsal process and, as explained below, probably a small portion of its anterior, symphyseal region that included the anteriormost tooth. There is seemingly very little missing

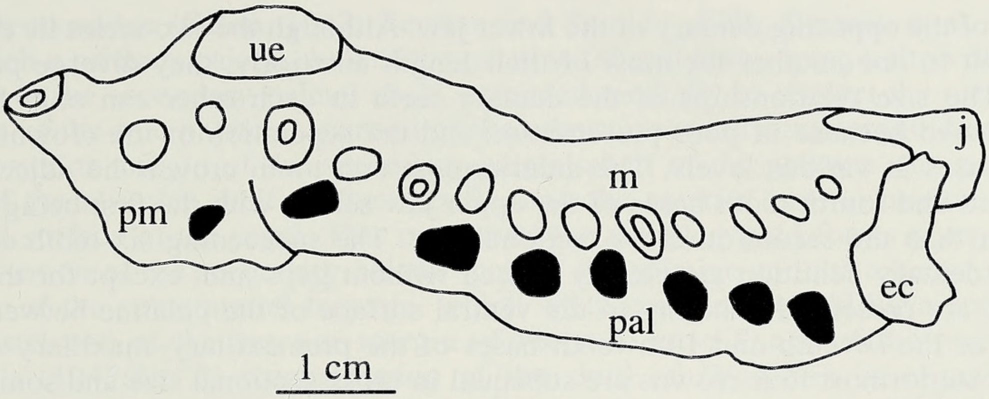

Fig. 2.—*Diadectes* sp. (AMNH 4346), holotype of *Helodectes paridens*. Outline drawing of Figure 1B to identify marginal dentitions of upper and lower jaws. Incomplete teeth shown as cross-sectional outlines drawn at level in which preservation ends. Ankylosed premaxillary–maxillary tooth bases shown as open outlines and isolated dentary tooth crowns as filled-in outlines. Abbreviations as in Figure 1.

from the maxilla except for the crowns of its teeth, although poor preservation makes it impossible to define all of its borders.

The marginal dentition is undoubtedly the most important and interesting aspect of AMNH 4346. Cope's (1880) original description of the holotype of *Helodectes paridens* (AMNH 4346) focused on what he believed to be its unique possession of two rows of marginal teeth. It is now quite apparent that the outer or lateral row, consisting of 14 teeth, is the only series of teeth ankylosed to the premaxilla and maxilla. All that remains of this series of teeth are the bases. Those of the first three teeth are subcircular in horizontal section and decrease serially in size posteriorly, with the third being markedly smaller than the two preceding it. The base of the fourth tooth is equal to the first in basal diameter and has a slightly transverse, oval outline, whereas the fifth tooth base is considerably smaller than the fourth and circular in outline. The bases of the succeeding teeth gradually increase in size, particularly in becoming transversely oval, to the tenth, whereas those of the last four teeth, which are noticeably the smallest of the entire series, gradually decrease serially in size posteriorly. In occlusal view the premaxillary–maxillary tooth row forms a slightly sigmoidal curve, with the anterior half of the series forming a labially convex curve and the posterior half forming a lingually convex curve. The bases of the oval, midseries cheek teeth are not oriented directly transversely, as the labial edges are slightly in advance of the lingual edges. Although the premaxillary–maxillary suture cannot be traced across the entire alveolar surface, it probably passed between the third and fourth preserved tooth bases. This determination is based in part on the fact that in *Diadectes* jaws examined by us, the last premaxillary tooth is typically much smaller than the preceding teeth of the premaxilla and the first tooth of the maxilla. Because the premaxilla of North American *Diadectes* possesses four teeth, it is also reasoned that the first tooth and the symphyseal portion of the premaxilla surrounding it have been lost. If this analysis is correct, the total tooth count for the upper jaw is four premaxillary and 11 maxillary teeth, which is the standard count for *Diadectes*.

Medial to the premaxillary–maxillary tooth row is a row of eight teeth, or more accurately their crowns, that undoubtedly represents a portion of the marginal series of the opposing dentary of the lower jaw. Although the two series lie closely adjacent to one another for most of their length anteriorly, they diverge posteriorly. The size relationships of the dentary teeth to each other can only be approximated because of poor preservation and the separation of the crowns from their bases at various levels. The anteriormost two tooth crowns lie adjacent to the third and fourth tooth bases of the upper jaw series, with the first being much smaller than the second in cross-sectional size. The succeeding six tooth crowns of the dentary dentition are closely spaced without gaps and, except for the first crown, are preserved adhering to the ventral surface of the palatine between the levels of the seventh and 14th tooth bases of the premaxillary–maxillary series. The posteriormost four crowns are subequal in cross-sectional size and somewhat expanded transversely, with the labial edge of each lying slightly in advance of the lingual edge. Whereas the two crowns preceding the posteriormost four are substantially larger, their margins are too incomplete to determine outline shape. Very little information about the morphology of the crowns is available, because they are closely attached to the bone of the upper jaw and palate and are too closely spaced to prepare fully. The second and fourth crowns are roughly single, conical cusps and are considerably longer than those of the succeeding dentary teeth. All that can be said of the remaining crowns is that those of the fifth and sixth are low and moderately expanded transversely, without any obvious appearance of medial or lateral cusps. The cross-sectional exposures of the teeth of both rows reveal a labyrinthine structure.

By way of comparison with North American *Diadectes* dentitions and considering the spatial relationships of the dentary crowns to the premaxillary–maxillary teeth, the first and second dentary crowns in AMNH 4346 likely represent the third and fifth tooth positions of the complete series. Continuing, if the gap following the second preserved tooth crown is considered equivalent to two teeth, then the remaining six posteriormost crowns represent the eighth through 13th tooth positions of the complete series. If this analysis is correct, then probably somewhere between one and five posteriormost dentary teeth are not represented, as, according to Welles (1941), the number of lower jaw teeth in *Diadectes lentus* from the Early Permian Wichita Group of Texas varies from 14 to 18. However, because the dentaries of small or juvenile specimens of *Diadectes* generally contain fewer teeth than those of adults, it is suspected that the number in AMNH 4346 was probably 14 or possibly 15. As an example, in the skull of the small, immature specimen *Diadectes sanmiguelensis* MCZ 2989 from the Lower Permian Cutler Formation of Colorado (Lewis and Vaughn, 1965), the dentary possesses a total of 14 teeth.

A small, badly weathered portion of the lacrimal remains articulated with the dorsal lamina of the maxilla, but the union is visible only on the medial surface of AMNH 4346. Only the anterior end of the jugal, where it contacts the maxilla along the jaw margin, is preserved and includes, as Cope (1880) noted, a small portion of its entrance into the orbital rim. The incomplete palatine is represented mainly by a narrow, arcuate shelf of bone that extends ventromedially from its contact with the inner margin of the maxillary alveolar shelf. This portion of the palatine is referred to as the secondary palatal shelf by Olson (1947) and Berman and Sumida (1995), and, although its suture with the maxilla cannot be discerned, it is most easily located in AMNH 4346 by the row of six tooth crowns of the dentary adhering to its ventral surface. Undoubtedly, the complete palatine of AMNH 4346 was identical to those in North American and German *Diadectes* and *Desmatodon* (Olson, 1947; Berman and Sumida, 1995; Berman et al., 1998) in which a primary palatal shelf of the palatine (absent here), lying a short distance dorsal to the secondary palatal shelf, extended medially to contact the pterygoid as part of the true palate. A portion of the otherwise small ectopterygoid contacts the posterior margin of the secondary palatal shelf of the palatine, the posterior end of the alveolar shelf of the maxilla, and the anterior ventral margin of the medial surface of the jugal. This portion of the ectopterygoid forms a very short continuation of the secondary palatal shelf of the palatine and the anterior medial border of the subtemporal fenestra, which when complete would have contacted the distal end of the anterior margin of the transverse flange of the pterygoid. Olson's (1947:fig. 3) reconstruction of the skull of *Diadectes* in ventral view clearly depicts these structural relationships of the ectopterygoid, although the jugal is mislabeled as the squamosal.

A SECOND EXAMPLE OF *HELODECTES*-LIKE DENTAL PRESERVATION

A pair of opposing upper and lower, left jaw elements (Fig. 3), belonging to a single *Diadectes* specimen, provides indisputable evidence for the above interpretation of the double row of marginal teeth in the holotype of *Helodectes paridens*. Both jaw fragments are part of a large collection of undescribed, isolated, tooth-bearing jaw and mainly disarticulated postcranial elements representing at least three extremely small juveniles of *Diadectes* from the Lower Permian Wichita Group of Texas that were collectively catalogued as MCZ 2780 without specific assignment. For the purpose of description, however, the two jaw fragments which are the focus here have been recatalogued as MCZ 9331. They not only duplicate the double-toothed row condition in AMNH 4346, but most importantly can be rejoined in their original, preserved position to demonstrate that one of the two rows of teeth in each jaw represents the crowns of the opposing jaw dentition.

The upper left jaw fragment of MCZ 9331 (Fig. 3) includes essentially the entire maxilla, a small portion of the jugal that extends between its contact with the posterior dorsal margin of the maxilla and the anteroventral rim of the orbit, most of the lacrimal, and at least the greater portion of the secondary palatal shelf of the palatine. Although a series of 12 maxillary teeth is represented (Fig. 3C, 4A), the first and last teeth are represented by empty alveoli, teeth 2 through 4 and 6 through 9 are variably incomplete, teeth 5 and 10 are partially erupted crowns, and only tooth 11 is essentially complete. All of the teeth except possibly the last two appear to exhibit some transverse expansion, with those of the mid-series region being the most expanded. The crown of a replacement tooth is visible in the lingual pit of the third tooth. It is possible that the partial alveolus at the anterior end of the maxilla actually held the posteriormost premaxillary tooth, as the maxilla of *Diadectes* typically possesses 11 teeth. Although poor preservation makes it difficult to describe serial size changes in the maxillary teeth, some general remarks are possible. On the basis of their basal diameters, the anteriormost and largest teeth of the series decrease serially in size posteriorly to about the fifth tooth, the succeeding three teeth are subequal, and the last four teeth exhibit a noticeable serial decrease in size posteriorly. Lying medially adjacent to maxillary teeth 7 through 11 and adhering to the ventral surface of the secondary palatal shelf of the palatine is a series of four, closely spaced crowns belonging to teeth 7 through 10 of the marginal dentition of the opposing lower jaw dentary.

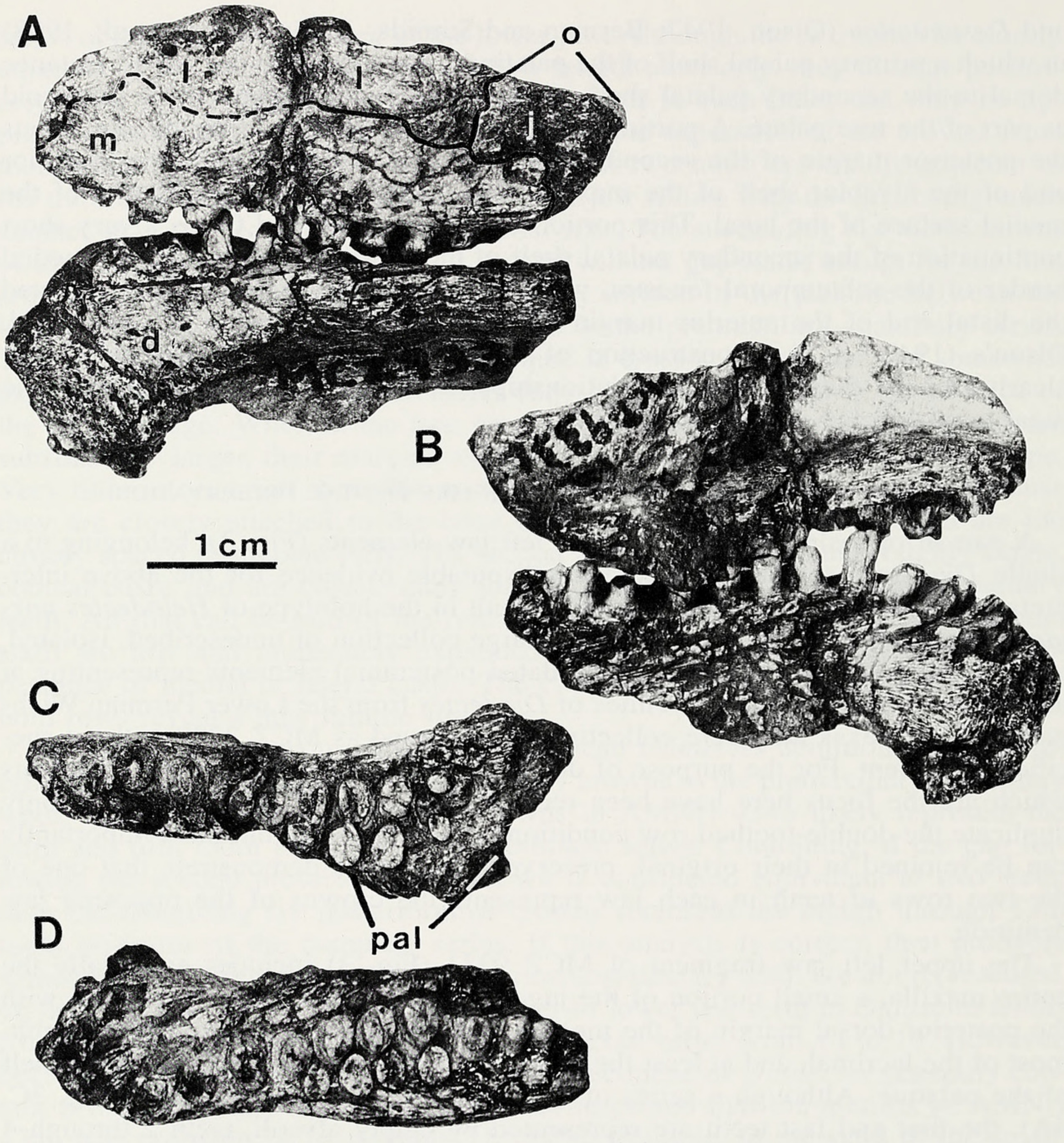

Fig. 3.—*Diadectes* sp. (MCZ 9331). A, lateral, and B, medial views of upper and lower jaw fragments joined in original preserved position. C and D, upper and lower jaw fragments, respectively, in occlusal (anterior to left) view. Abbreviations: d, dentary; j, jugal; l, lacrimal; m, maxilla; o, orbital rim; pal, secondary palatal shelf of the palatine.

Serial identifications of the separated dentary tooth crowns, as well as those of the maxilla adhering to the dentary discussed below, are easily determined, as the two jaws can be rejoined so that all the crowns except that of the 12th maxillary tooth contact in an exact union the tooth bases of their origin.

The lower jaw fragment of MCZ 9331 (Fig. 3) includes only the dentary, which appears to be missing mainly a small portion of its posterior end. A continuous row of 12 tooth bases extends the length of the alveolar shelf (Fig. 3D, 4B). As the small margin of the shelf posterior to the last tooth does not exhibit any signs of additional teeth, the entire marginal series of the dentary may be represented. Typically, however, the dentary of *Diadectes* held at least 14 teeth. Using basal

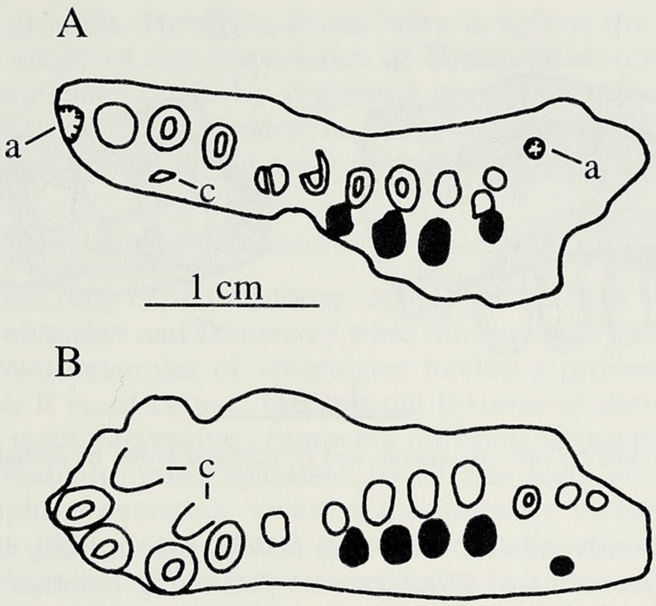

Fig. 4.—*Diadectes* sp. (MCZ 9331). Outline drawings of Figure 3C and D to indicate marginal dentitions of upper and lower jaws. Ankylosed maxillary and dentary tooth bases of A and B, respectively, shown as open outlines and separated dentary and maxillary tooth crowns of A and B, respectively, shown as filled-in outlines. Abbreviations: a, empty alveolus; c, crown of replacement tooth.

diameter as an indication of size, in general the first five teeth, which included the largest of the series, decrease serially in size posteriorly, the succeeding four teeth are noticeably smaller and exhibit a modest serial increase in size posteriorly, and the last three teeth, the smallest of the series, decrease serially in size posteriorly. The anterodorsal inclination of the first four tooth bases indicates that these teeth were procumbent as in *Diadectes*. The crowns of replacement teeth in the lingual pits of the first and third teeth also indicate that the first four teeth were *Diadectes*-like in being bluntly spatulate and incisiform. Lying immediately lateral to teeth 6 through 9 is a series of four closely spaced crowns belonging to teeth 6 through 9 of the marginal dentition of the opposing upper jaw maxilla. Following a small gap, a fifth crown belonging to the 12th maxillary tooth lies a short distance labial to dentary tooth 11.

DISCUSSION

Taxonomic Status of Helodectes

Restudy of the Early Permian holotype of *Helodectes paridens* AMNH 4346 clearly indicates that it should be regarded as a junior synonym of *Diadectes* of the same age. The poorly preserved bones of the left side of the skull that comprise AMNH 4346 deviate in no recognizable way from those in *Diadectes*. Most noteworthy, the unusual structure of the palatine, specifically the presence of the secondary palatal shelf, is known elsewhere only in *Diadectes* and the very closely related Late Pennsylvanian *Desmatodon* (Olson, 1947; Berman and Sumida, 1995). The extremely small size of AMNH 4346, as well as the *Diadectes* specimens MCZ 2780 and 9331, represents an early ontogenetic stage of growth seldom encountered and rarely described in this genus (Olson, 1947; Lewis and Vaughn, 1965; Berman and Sumida, 1995). Small size combined with concomitant differences in skeletal proportions and dental features from those of adult

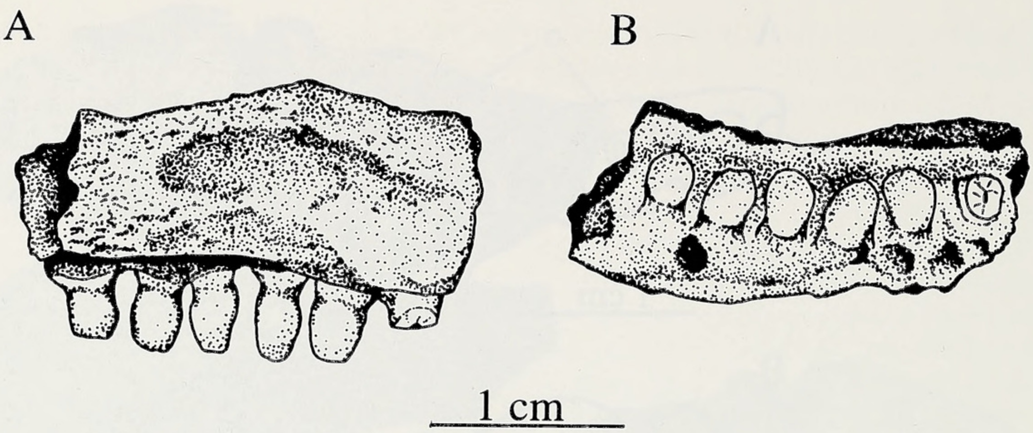

Fig. 5.—*Diadectes* sp. (MCZ 2780). A, lateral, and B, occlusal views of partial right juvenile maxilla.

specimens undoubtedly misled, as Olson (1947) noted, early investigators to interpret juvenile specimens of *Diadectes* as pertaining to other genera. This confusion was partly resolved, however, with the recent description (Berman and Sumida, 1995) of the prominent, ontogenetic changes in the marginal dentition of *Diadectes*. That study clearly accounts for the differences between the dentition of AMNH 4346 and those of adult specimens of *Diadectes* as reflecting widely separated, ontogenetic growth stages. The dentition of juvenile specimens of *Diadectes*, including AMNH 4346, can be most easily distinguished from that of adults by the cheek teeth. In contrast to adults, the cheek teeth in juveniles do not exhibit extreme transverse expansion and molarization that results in the central cusp being flanked lingually and labially by a lower, but prominent, shoulder-like cusp. In order to emphasize this observation, Berman and Sumida (1995) stated that the maxillary and dentary cheek teeth in the very immature specimens of *Diadectes* MCZ 2780 (including MCZ 9331) and *D. sanmiguelensis* MCZ 2989 exhibit little transverse widening, and are more accurately described as bulbous, with a weakly developed central cusp and essentially no lingual or labial shoulder-like cusps (Fig. 5). Despite representing an early juvenile stage of development, the dentition of AMNH 4346 is still like that of adult specimens of *Diadectes* in duplicating in greater or lesser degree numerous features of the teeth, such as their number, arrangement, morphology, and serial changes (Case, 1911; Lewis and Vaughn, 1965; Berman and Sumida, 1995).

AMNH 4346 might be suspected of being a juvenile specimen of the rare, Late Pennsylvanian *Desmatodon*, whose cranial anatomy, including its dentition, is nearly identical to that of the later-occurring *Diadectes* (Vaughn, 1972; Berman and Sumida, 1995). The potential for this confusion, however, is confidently eliminated by considering the subtle differences in the juvenile dentitions of these two genera first noted by Vaughn (1972) and later more fully documented by Berman and Sumida (1995). They list four dental features of the juvenile maxilla in *Desmatodon* which are absent or greatly reduced in mature specimens of this genus and apparently not present in specimens of *Diadectes* of any age: 1) fewer number of teeth, 2) greater relative spacing of teeth, 3) first two maxillary teeth relatively longer and more incisiform, and 4) absence of wear facets. Features 1 and 2 clearly identify AMNH 4346 as *Diadectes*, whereas poor preservation prevents the use of features 3 and 4.

Specific assignment of AMNH 4346 and MCZ 2780 and 9331 is impossible on morphological grounds. However, if one were to follow the recommendations in Olson's (1947) study of the systematics of Diadectidae, tentative assignment to *Diadectes sideropelicus* could be suggested on stratigraphic grounds, as it is the only species that he recommended be recognized from the Wichita beds of Texas until such evidence to the contrary is described.

Occlusion of Diadectid Marginal Dentitions

On the basis of not only dental anatomy, but also features of the entire skeleton, the diadectids *Desmatodon* and *Diadectes* were interpreted by Hotton et al. (1997) as the earliest known examples of vertebrates having a primarily high-fiber diet of terrestrial plants. It is, of course, the unusual features of their dentitions which have provided the most persuasive arguments for considering them as herbivores. The anterior, procumbent, rather spatulate, incisiform teeth are ideally suited for grasping and cropping vegetation, whereas the uniquely molariform cheek teeth are indicative of a highly specialized masticatory structure for dealing with a tough, high-fiber plant diet. Wear patterns confirm a vertical motion of the anterior incisiform teeth and a backward or propalinal motion of the lower jaw cheek teeth against those of the upper jaw during occlusion and mastication (Hotton et al., 1997).

The unusual preservation of the dentitions of AMNH 4346 and MCZ 9331 prompts speculation of other aspects of the occlusion of the cheek teeth in *Diadectes* and *Desmatodon*. In the extremely small marginal dentitions of AMNH 4346 and MCZ 2780 and 9331 most of the crown tips of the cheek teeth are either not exposed or are too poorly preserved to reveal wear facets. In a few instances, however, the crowns in MCZ 2780 are exposed and preserved well enough to note that attrition is either absent or limited to small, subcircular facets on the lingual and labial surfaces of the upper and lower cheek teeth, respectively. The pattern of wear is greatly restricted, despite the cheek teeth being bulbous to moderately expanded transversely, and could have been achieved only if occlusion was restricted to contact between the labial surfaces of the lower and the lingual surfaces of the upper cheek teeth during propalinal movement of the lower jaw. The absence of attrition on the tips of the crowns, however, does not necessarily indicate that they did not participate directly in the mastication of food. To the contrary, there are several features of AMNH 4346 and MCZ 9331 which suggest strongly an additional, occlusal component of the cheek teeth that involves the crown tips. The most persuasive feature is the side-by-side preservation of their upper and lower dentitions, with the crown tips of the dentary cheek teeth contacting the ventral surface of the secondary palatal shelf of the palatine and the crown tips of the maxillary cheek teeth contacting the dentary lateral to its dentition. If considered in combination with the limited attrition pattern of the cheek teeth, then it seems very plausible that the above associations of the crown tips of the dentary and maxillary cheek teeth with the palatine and dentary, respectively, indicate an additional, important masticatory component of the cheek teeth. Additionally, in AMNH 4346 and MCZ 9331 the secondary palatal shelf of the palatine curves strongly ventromedially, creating a channel-like space between it and the lingual surfaces of the maxillary cheek teeth. Therefore, it is very likely that the lingual margins, as well as the crown tips, of the cheek teeth of the maxilla contacted the secondary palatal shelf during mastication.

If occlusion of the dentary cheek teeth with the palatine is accepted, it forces a reconsideration of previous interpretations of the functional role of the secondary palatal shelf of the palatine. Commenting on this unique structure in *Diadectes*, now known to occur also in *Desmatodon* (Berman and Sumida, 1995), Olson (1947:16) noted that the "ventral surface of the process is rough and there usually are a few small teeth along its posterior margin. This has been the basis for considering its primary function as masticatory" by earlier authors. Olson was convinced, however, that the secondary palatal shelf more probably represents the incipient development of a secondary palate. Crucial to the interpretation of this structure is an excellently preserved, isolated palatine of *Desmatodon* (CM 47674) described in detail and as identical to that in *Diadectes* by Berman and Sumida (1995). The ventral surface of the secondary palatal shelf was characterized (Berman and Sumida, 1995:322–323) as "distinctly sculptured by short, shallow, irregular channels and low ridges, and a few, scattered, minute tubercular prominences." The coarse sculpturing of the secondary palatal shelf suggests the presence of a tough, perhaps keratinized, tissue covering. This would have provided an ideal masticatory surface for the dentary cheek teeth. Also pertinent to this discussion is the description (Berman and Sumida, 1995) of a shagreen of denticles distributed over areas of the posterior portion of the channel formed between the primary and secondary palatal shelves of the palatine in *Desmatodon*. This was interpreted as contradictory evidence of Olson's (1947) theory that the secondary palatal shelf represents a partially developed secondary palate.

A twofold, occlusal pattern of the maxillary cheek teeth during mastication, similar to that suggested for the dentary cheek teeth, can also be hypothesized. In specimens of *Diadectes* and *Desmatodon* having complete dentaries there exists an unusual, unique structure that suggests the possible presence of a specialized masticatory surface. Lateral to the bases of the cheek teeth is a shallow groove whose outer wall is formed by a vertical extension of the lateral surface of the dentary into a thin, flange-like ridge or parapet (Welles, 1941; Vaughn, 1972; Berman and Sumida, 1995). Welles (1941:424) remarked that "this flange resembles that of the Chelonia and Anomodontia and could very well have served a similar purpose; that is, to support a horny cutting beak." This interpretation, however, is susceptible to the observation that the outer surface of the parapet exhibits the same coarse surface sculpturing that occurs over the entire lateral surface of the lower jaw. That is, there is no distinct change in the bone texture along the outer jaw margin to support the presence of a horny beak, although this does not preclude a cropping function of the parapet. More important to the discussion here, however, is the channel-like basin formed between the parapet and the cheek teeth, as it approximates the occlusal position of the crown-tips and labial margins of the maxillary cheek teeth. Therefore, the parapet of the dentary not only closely duplicates that of the secondary palatal shelf of the palatine in structure, but probably also functioned as a masticatory surface. The internal surface of the parapet, which also forms the outer margin of the floor of the channel-like basin, is coarsely sculptured in a manner very similar to that of the secondary palatal shelf of the palatine and conceivably could have been covered also by a tough, keratinized tissue. In this connection, it is suspected that both the crown tips and labial margins of the maxillary cheek teeth contacted the inner surface of the parapet and channel during mastication. Although incomplete preservation prevents identification of a parapet and groove lateral to the dentary cheek teeth in the juvenile specimens MCZ 2780 and 9331, these structures are present in *D. sanmiguelensis* MCZ 2989 (Lewis and Vaughn, 1965) which is

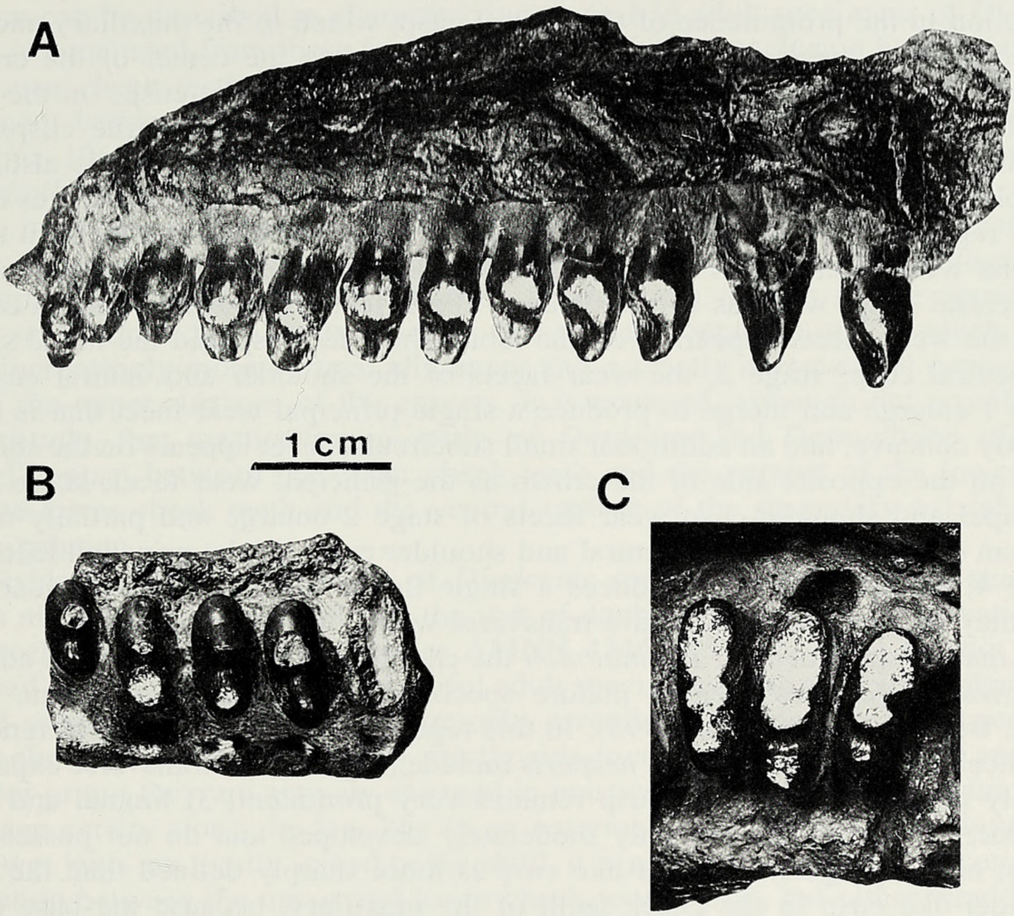

Fig. 6.—Maxillary dentitions of adult *Desmatodon* and *Diadectes* specimens to illustrate attrition patterns of cheek teeth. A, medial view of left maxilla of *Desmatodon hesperis* (CM 47654); B, occlusal view of portion of left maxilla (anterior to left) of *Desmatodon hollandi* (CM 1938) containing teeth 5–8 and the root of 9; and C, occlusal view of portion of right maxilla (anterior to left) of *Diadectes lentus* (UC 675) showing teeth 7–9. Wear facets have been whitened.

approximately the same size. The cheek teeth of MCZ 2989 also exhibit the same reversed pattern of attrition that does not include the crown tips (Lewis and Vaughn, 1965).

Some confirmation on the above hypothesis of occlusion of the cheek teeth of diadectids can be found in the dentition of the nearly complete juvenile right maxilla of *Desmatodon hesperis* CM 47668 (formally UCLA VP 1748) described by Vaughn (1972). By way of comparison, its estimated length of about 55 mm is perhaps only 5 mm greater than that of the maxilla in AMNH 4346. With regard to this discussion, most notable about the maxillary dentition in CM 47668, consisting of eight complete teeth representing the entire series, is the absence of any signs of attrition. This might indicate that during mastication there was little or no direct occlusion between the upper and lower cheek teeth, but rather they occluded principally with the inner surface of the lower jaw parapet. As was pointed out by Vaughn (1972), rapid tooth replacement offers an alternative but less satisfactory explanation for the absence of wear facets in CM 47668.

In the development to full maturity the cheek teeth of *Diadectes* undergo a number of profound morphological changes that result in a much greater degree of molarization (Fig. 6C): 1) dramatic increase in transverse expansion; 2) strong reduction in the prominence of the central cusp, which in the maxillary and dentary dentitions occupy positions labial and lingual to the center of the crowns, respectively; and 3) development of prominent, shoulder-like cusps on the labial and lingual margins of the crown which subsequently acquire true cusps. The attrition pattern of the cheek teeth in adult specimens of *Diadectes* is also more complicated than in juveniles and progresses typically through four stages before tooth replacement occurs (Fig. 6C): **stage 1**, in the maxillary cheek teeth a subcircular wear facet occurs on the lingual shoulder cusp and on the lingual side of the central cusp, whereas in the dentary cheek teeth the reverse pattern occurs, with the wear facets appearing on the labial shoulder cusp and the labial side of the central cusp; **stage 2**, the wear facets of the shoulder and central cusps of stage 1 enlarge and merge to produce a single principal wear facet that is flat or slightly concave, and an additional small subcircular facet appears on the shoulder cusp on the opposite side of the crown as the principal wear facet; **stage 3**, the principal and shoulder-cusp wear facets of stage 2 enlarge and partially merge, with an eventual loss of the central and shoulder cusps of the principal facet; and **stage 4**, extreme attrition produces a single flat or slightly concave wear facet that may extend nearly the entire transverse width of the crown.

In mature specimens of *Desmatodon* the cheek teeth never acquire the advance molarization features seen in mature specimens of *Diadectes* (Vaughn, 1969, 1972; Berman and Sumida, 1995). In this regard, the most notable differences of the cheek teeth of *Desmatodon hesperis* include (Fig. 6A): 1) transverse expansion is only moderate; 2) central cusp remains very prominent; 3) lingual and labial shoulders of the crown are only moderately developed and do not possess true cusps; and 4) lingual, shoulder-like cusp is more sharply defined than the labial shoulder-like cusp in the cheek teeth of the maxillary, because the base of the central cusp is much more expanded laterally than it is medially, whereas the reverse condition is true in the cheek teeth of the dentary. Along with a lesser degree of molarization, the degree of attrition of the cheek teeth in adult specimens of *D. hesperis* is limited to a subcircular facet on the lingual and labial shoulder-like cusps in those of the maxilla and dentary, respectively (Fig. 6A). It is also interesting that in adult specimens of *D. hesperis* almost all of the maxillary cheek teeth exhibit attrition, whereas only rarely do those of the dentary. As examples, in the complete dentition of the holotypic left maxilla CM 47654 (Fig. 6A; formally UCLA VP 1706) and in the five cheek teeth of the partial right maxilla CM 47677 of *D. hesperis* a distinct wear facet occurs on all the teeth except for two far posterior cheek teeth in CM 47654 (Vaughn, 1969, 1972). This is contrasted by the complete dentitions of the right lower jaw CM 47670 and left dentary CM 47676 of *D. hesperis* in which the number of cheek teeth exhibiting wear facets is only three and one, respectively (Berman and Sumida, 1995:fig. 3, 4). The above features of attrition suggest that occlusion between the upper and lower cheek teeth was not only restricted to a lingual–labial or side-to-side contact, but, as suggested by the dentary dentitions, in some instances was greatly reduced and, therefore, similar to the condition in very juvenile specimens of *Diadectes*. In the four cheek teeth of the presumed adult holotypic left maxilla CM 1938 (Fig. 6B) and only-described specimen of *D. hollandi* the degree of molarization and attrition is basically intermediate between those of *D. hesperis* and adults of *Diadectes*. Greater transverse expansion of the cheek teeth in CM 1938 is accompanied by reduction in the prominence of the central cusp and the development of well-defined labial and lingual shoulders that lack true cusps, and attrition can be described as characterizing stage 1 in adult specimens of *Diadectes*. It is concluded from these features that in CM 1938 occlusion between upper and lower cheek teeth had begun to shift to a principally dorsoventral, vertical alignment between the upper crown surfaces. This agrees with the observation (Vaughn, 1969, 1972; Berman and Sumida, 1995) that the cheek-tooth dentition in *D. hollandi* is more advanced than that in *D. hesperis*.

The preceding discussion suggests that with the increased transverse expansion of the cheek teeth in *Diadectes* and *Desmatodon*, either as a result of ontogenetic development or evolution, the occlusion between the crowns of the upper and lower series shifts from an exclusively side-to-side contact to one in which there is an increasingly more vertical alignment and a strictly dorsoventral contact between the upper surfaces of the crowns. It is assumed, although not possible to demonstrate, that mastication in adults of *Diadectes* and *Desmatodon* still involved contact between the upper cheek teeth and the parapet of the lower jaw and the lower cheek teeth and the ventral surface of the secondary palatal shelf of the palatine.

Considering the large number of *Diadectes* specimens available for study, it seems more than coincidental that the sort of double-toothed row preservation of the cheek teeth seen in the juveniles AMNH 4346 and MCZ 9331 has not been reported in any of the far more plentiful adult specimens. The obvious explanation would seem to be that only in extremely juvenile specimens do the upper and lower cheek-tooth series occupy a strictly side-to-side relationship to one another, whether or not they are actively engaged in mastication. If, therefore, postmortem breakage occurs along the jaw line in an extremely juvenile specimen in which the lower jaws are tightly joined to the skull, it is not likely to result in a complete separation between the upper and lower cheek-tooth series, but rather would produce the double-toothed row condition seen in AMNH 4346 and MCZ 9331. On the other hand, under the same circumstances adult specimens of *Diadectes* would not be expected to produce the same double-toothed row condition, as their opposing cheek-tooth series occlude exclusively between the upper crown surfaces. Although only rarely is it possible to examine the cheek teeth in a resting state of occlusion in a mature, undistorted specimen of *Diadectes*, one unusual example is available. The *Diadectes* skull CM 24127 from the Early Permian Washington Formation of West Virginia is uniquely preserved as an internal mold of an undistorted skull and mandible that faithfully reproduces anatomical features (Berman, 1971). Most importantly, the lower jaws are in their proper orientation, so that the resting, occlusal state of the upper and lower cheek teeth can be clearly interpreted. Although the lateral margin of the dentition is not represented, latex casts allowed a detailed description of all other aspects of the cheek-tooth series (Berman, 1971). Not only do they exhibit an advanced stage of molarization and a reversed pattern of attrition, with many teeth attaining at least an advanced stage 3 of wear, but also a large degree of dorsoventral occlusion between the upper surfaces of the opposing crowns.

Hotton et al. (1997) presented a compelling argument that *Diadectes*, as well as *Desmatodon*, was primarily adapted to a diet of high-fiber terrestrial vegetation. Their evidence relied almost exclusively on the complex dental adaptations that allowed for the collection and mechanical processing of a wide variety of plant tissues. It was also argued that the large size and body proportions of diadectids, particularly their bulky, rotund torsos, are suggestive of the possession of a disproportionally large gut needed for the endomicrobial fermentation of plant cellulose. The conclusions of Hotton et al., however, were obviously based on observations of adult specimens, and, as noted above, juveniles of *Diadectes* exhibit striking differences in their cheek dentitions and the manner in which they occluded. In particular, the cheek teeth of juveniles are far less molariform and the area of occlusion is not only much more limited in area, but is restricted to the lingual and labial, rather than the dorsal, margins of the crowns, and thus must have been far less effective in the comminution of plant tissues. These comparisons raise the question of whether the dentition of juvenile *Diadectes* was capable of processing terrestrial vegetation as efficiently and of equivalent toughness or fiber content as that consumed by adults. Changes in the dentition from juveniles to adults are too great not to suspect that they were not accompanied by a change in diet; perhaps the juveniles were primarily insectivorous or were omnivorous but restricted to low-fiber vegetation. Thus, our interpretation of the ontogeny of diadectid dentition and mastication lends strong support to preliminary observations by Vaughn (1972:25) that changes in the maxillary dentition in *Desmatodon hesperis* from juvenile to adult may have paralleled a shift in dietary habit.

Acknowledgments

The authors wish to express their thanks to the American Museum of Natural History and the Museum of Comparative Zoology for the loan of specimens.

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