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OROMYCTER, A NEW CASEID FROM THE LOWER PERMIAN OF OKLAHOMA

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ABSTRACT—Superbly preserved skeletal elements of the new taxon *Oromycter dolesorum* from the Lower Permian deposits in the Dolese Quarry, near Richards Spur, Oklahoma, record the earliest known evidence of a member of Caseidae. Although found as isolated elements, there is strong circumstantial evidence that the maxillae, premaxillae, lacrimal, and dentary belonged to a single individual. Isolated axial and appendicular elements from this locality are also tentatively attributed to this new form.

Caseasaur autapomorphies of *Oromycter* include the presence of the premaxillary rostral process, indirect evidence for an external shelf on the nasal, and lateroventrally tilted external maxillary surface. Caseid autapomorphies include the anterodorsally oriented maxillary process, the short, tall lacrimal, typical caseid ornamentation on the lacrimal, procumbent anterior dentition, largest teeth located anteriorly on each bone, and spatulate, lingually curved marginal dentition. However, the available evidence indicates that *Oromycter* is a sister taxon to all other caseids because it lacks the leafy serrations on the teeth, has a relatively long lacrimal bone, has a larger number of marginal teeth than most other caseids, lacks an external narial shelf on the maxilla while one is poorly developed on the lacrimal. The presence of this early, basal member of the Caseidae at the Dolese Quarry is consistent with the hypothesis that the initial evolutionary history of this group of herbivores occurred away from the typical deltaic, floodplain depositional environments that preserve the majority of the known Permo-Carboniferous terrestrial vertebrate communities.

INTRODUCTION

Caseids are unique among Permo-Carboniferous synapsids in appearing late in the history of group, near the end of the initial evolutionary radiation of the mammal-like amniotes (Reisz, 1986). Four of the six major clades of Permo-Carboniferous synapsids appear in the fossil record before the end of the Carboniferous. These include the varanopids (Reisz and Dilkes, 2003; Anderson and Reisz, 2003), a group of basal eupelycosaurs whose fossil record extends from the Late Pennsylvanian to the top of the Middle Permian (Kazanian/Tatarian boundary), and the more crownward ophiacodontids (Reisz, 1972), whose fossil record extends from the Middle Pennsylvanian to the Early Permian. In addition, the small to very large, herbivorous edaphosaurids (Modesto and Reisz, 1992) also have a fossil record that extends from the Late Pennsylvanian to the Early Permian. The sphenacodontids (Berman et al., 2001), the dominant terrestrial predators of their time, have a fossil record that extends from the latest Pennsylvanian, or possibly the Middle Pennsylvanian if the identification of fragmentary remains from Florence, Nova Scotia is correct (Reisz, 1972), to the end of the Early Permian. In contrast, the Eothyrididae and Caseidae, the two stem synapsid taxa that form the Caseasauria, only appear in the fossil record during the Early Permian.

Only two forms, *Eothyris* from the Early Permian of Texas and *Oedaleops* from the Early Permian of New Mexico, represent the Eothyrididae. These two taxa are known only on the basis of the holotypic skulls and two additional cranial fragments of *Oedaleops*. Clearly, members of this particular clade are rare components of the contemporary faunal assemblages, and any interpretation of the stratigraphic or temporal range of this group is suspect. The available evidence does indicate that these synapsids were small carnivores with large, well-developed caniniform teeth and slightly recurved, piercing marginal dentition.

The fossil record of the Caseidae is unusual because skeletal remains of these forms only appear in the Upper Leonardian (later part of the Lower Permian) but quickly become the most commonly found synapsids of their time. The oldest known caseid, *Casea broili*, has been recovered from the fossilliferous site called the *Cacops* bone bed, from Indian Creek, Baylor County, Texas. Caseids were relatively common elements of the uppermost Lower Permian (Leonardian) sediments of Texas and Oklahoma, and have also been found in Middle Permian (Guadalupian) sediments of Oklahoma. The fossil record of this clade of stem synapsids extends well into the upper part of the Middle Permian, and the caseid *Ennatosaurus* has been recovered from Mezen and Pinega, localities that straddle the Kazanian/Tatarian boundary in Northern Russia.

Previous phylogenetic analyses (Reisz et al., 1998) have shown that the ghost lineage of caseid synapsids is unusually long, with a large temporal gap between the earliest known appearance of caseids and their minimum divergence time from their sister taxon, the eothyridids. Consequently, little is known about the origins and early evolutionary history of this interesting group of herbivorous animals. Partly in order to explain this gap in our knowledge of the group, E. C. Olson (Olson 1968:313–319) suggested that the early evolutionary history of this group occurred as part of a distinct terrestrial community (his so-called chronofauna) away from the common areas of deposition, the lowland/deltaic regimes of the Early Permian.

The skeletal elements described here were found in 1984 by Dr. John Bolt at the Dolese Bros. Quarry, at Richards Spur, near Fort Sill, Oklahoma. The precise age of Dolese Quarry fossilliferous sediments is difficult to determine, and most previous interpretations have been based on the composition of its terrestrial vertebrate fauna (Sullivan and Reisz, 2000). However, Modesto (1998) has referred to the limestones that contain the terrestrial sediments as being circumscribed by the upper horizons of the Early Permian Garber Formation (Sumner Group, Leonardian). Despite their fragmentary nature, there is evidence to suggest that the cranial elements described here may have been derived from a single individual: 1) All have been found in a single lump of sediment, 2) all elements are of the size consistent with a single individual, and 3) there is no duplication of cranial elements. Nevertheless, in the absence of definite articulation, all specimens were given different numbers.

This discovery is significant because these skeletal elements

clearly belonged to a caseid that can be considered to be the most basal member of the clade. In addition, this earliest known caseid comes from the only known true upland Paleozoic depositional regime in North America, the fissure fills of the Early Permian Slick Hills, Oklahoma. The discovery of the oldest known, most basal caseid in this unusual depositional environment has important implications for synapsid evolution, and the evolution of herbivory.

SYSTEMATIC PALEONTOLOGY

SYNAPSIDA Osborn, 1903
CASEASAURIA Williston, 1911
CASEIDAE Williston, 1911

Definition—A stem-based definition of this group includes all taxa more closely related to *Casea* or *Cotylorhynchus* than to *Eothyris*.

Revised Diagnosis—Caseasaurian synapsids with largest marginal teeth located anteriorly in tooth row, first premaxillary in upper row and first dentary in lower row, respectively. All subsequent teeth decreasing gradually in size, without caniniform. Each marginal tooth with lingual shoulder and spatulate distally, with lingual rather than posterior curvature near tip. Lacrimal reduced in length, and extensively covered by anterodorsal process of maxilla. Narial shelf extending onto lacrimal. External narial opening greatly enlarged dorsoventrally, dorsoventral height of its external border being at least 2/3rds height of orbit.

OROMYCTER, gen. nov.

Etymology—*Oros*, mountain (Greek), in recognition of the upland depositional environment that is preserved at the Dolese Quarry; *mycter*, nose, snout (Greek), reflecting the enlarged narial opening that characterizes caseids.

Type and Only Known Species—*Oromycter dolesorum*, sp. nov.

Diagnosis—As for the type and only known species, given below.

OROMYCTER DOLESORUM, sp. nov.

Etymology—*Dolesorum*, referring to the Dolese Brothers, operators of the quarry near Richards Spur, Oklahoma, where the fossils were found.

Holotype—Left maxilla, FMNH (Field Museum of Natural History, Chicago) PR2281.

Referred Specimens—Right and left premaxillae, FMNH PR 2283 and 2284; left lacrimal, FMNH PR 2285; posterior fragment of right maxilla (FMNH PR 2282); anterior and posterior fragments of left dentary (FMNH 2286 and 2287); all found together with the holotype, but disarticulated. Found separately in different parts of the collection, and clearly representing additional individuals, phalanges (FMNH PR 2288) including terminal, claw bearing units (FMNH PR 2289); caudal vertebra (FMNH PR 2290).

Type Locality and Horizon—OMNH V51 (Oklahoma Museum of Natural History, Richards Spur Locality) Dolese Brothers limestone quarry (SW1/4 section 31, Township 4N, Range 11W), located about 10 km north of Fort Sill, Comanche County, Oklahoma. The fissure fill deposit is considered to be stratigraphically equivalent to the lowermost Clear Fork Group (Leonardian: Lower Permian) of Texas.

Diagnosis—Small caseid characterized by absence of distinct, distal, leaf-like serrations on teeth. Instead, spatulate, broad, distal end of each tooth with roughened cutting edge. Premaxilla with places for three teeth, maxilla with places for twelve. Maxilla lacking anterior narial emargination. Differing from all other caseids in proportions of lacrimal bone.

DESCRIPTION

Maxilla—A virtually complete left element (Fig. 1A) and a posterior fragment from the right side (Fig. 1B), show that the maxilla is stout, and has places for 12 teeth. The left maxilla was originally found in two pieces, separated by about 5 cm of gray matrix, on a small block that also contained the left lacrimal, one of the premaxillae, and the posterior fragment of the left dentary. Only a small anteroventral process of the alveolar shelf, and a small anterodorsal corner of the dorsal process of this bone are missing. The lateral surface of the maxilla is characterized by the presence of delicate sculpturing, and by the presence of a series of large, lateral, supra-alveolar foramina, of which the most anterior is oriented forward and is the largest. The next two foramina in the series are only slightly smaller than the first, but are oriented anteroventrally and ventrally, respectively. Since the matrix has been dissolved from this bone it was possible to determine that these foramina communicated with a large medial supra-alveolar foramen that is oriented posteromedially on the medial surface of the bone. As is the case with the first, large foramen on the lateral surface, this opening in the bone is continued on the surface of the bone as an elongate groove. The internal passages of the other foramina could not be determined because of their small size, but are also likely to have pierced the bone and to have opened medially near the central portion of the bone, at the level of the 4th–6th tooth. The last in the series of maxillary foramina opens posteriorly, as seen on both maxillae, and is also continued as a long, narrow groove.

The remainder of the maxillary lateral surface is covered by fine sculpturing and an elongate, slender sutural surface for the jugal bone. Perhaps the most diagnostic feature of this bone is the presence of a large anterodorsal process of the maxilla, forming a tall posterior border of the external naris. This process is present in all caseids, and is located at the level of the first three teeth of the maxilla. The anterior border of the naris is a simple edge, in strong contrast to younger, more crownward caseids where there is a distinct anterior notch that represents a ventral continuation of the external narial shelf that is found in all caseasaurs.

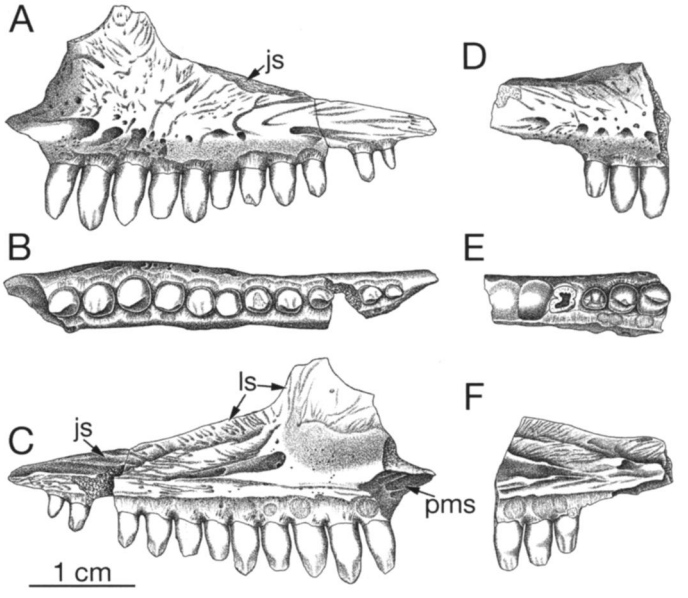

FIGURE 1. *Oromycter dolesorum*, gen. et sp. nov. **A–C**, left maxilla (FMNH PR 2281) in lateral, occlusal, and medial views; **E–F**, right maxillary fragment (FMNH PR 2282) in medial, lateral and occlusal views. Scale bar equals 1 cm. **Abbreviations**: **js**, jugal suture; **ls**, lacrimal suture; **pms**, premaxillary suture.

The ventral edge of the maxilla is only slightly convex, and bears the marginal dentition. A considerable amount of bone of attachment extends onto each tooth, and is dorsoventrally fluted where these two structures are joined together. This bone of attachment extends well beyond the normal edge of the maxilla both lingually and labially, and carries clearly formed resorption pits at the level of the first, third, and fourth maxillary tooth on the left maxillary. Incipient resorption pits are also present on the fragmentary right maxillary bone.

The medial surface is the most informative region of the maxilla, showing articular facets for the premaxilla along its anteroventral surface, and for the septomaxilla dorsally on the short anteroventral process of the bone. Most of the dorsal process of the maxilla shows attachment scars for the lacrimal bone. The area immediately posterior to the dorsal process represents an elongate sutural area for the rest of the lacrimal bone. The remainder of the posterodorsal region of the maxilla, above the alveolar shelf, is occupied by the sutural area for the jugal bone. This is in contrast to the condition seen in *Cotylorhynchus* and other caseids, where the maxilla contributes to the orbital margin. The posterior half of the alveolar shelf is also covered with sutural scars where the palatine bone would have attached, but anteriorly it is smooth between the fifth and first tooth positions, showing the extent of the maxillary contribution to the internal naris.

Premaxilla—Both left and right elements are preserved, but only the more complete left element is illustrated (Fig. 2). These premaxillae not only carry the type of dentition that is found in caseids, but their general morphology is entirely consistent with caseid affinities. As best seen in dorsal view, there is a modest vomerine or palatal process that forms the concave anteromedial edge of the internal naris. Although missing most of the dorsal or nasal process, there is clear evidence that it was massive and was tilted anteriorly, as in other caseids and eothyridids. In typical caseid fashion there are also large anterior foramina on the external premaxillary surface. However, there also is a large foramen that opens dorsally at the base of the dorsal process of the premaxilla.

The lateral maxillary process has a large surface of articulation with the anterior process of the maxilla that would have covered much of the lateral surface of this bone. There are only three teeth, with the first being the largest. Although the second tooth appears to be longer than the first, this is only because the distal end of the first tooth is worn significantly from probable occlusion with the first dentary tooth. Judging from its basal diameter and its overall massiveness it was larger than the second premaxillary tooth. If these premaxillae belonged to the same individual as the maxillae, then the first premaxillary tooth is the largest, most massive tooth in the upper tooth row, as in other caseids. Extensive bone of attachment is present along the base of each tooth, and there are two resorption pits lingually at the level of the first and second teeth. Both the first and second teeth bear distal wear facets along their distal edge, indicating that they may have occluded with the first and second dentary teeth, perhaps for cropping vegetation.

Lacrimal—The lacrimal bone (Fig. 3) probably belonged to the same individual as the holotypic maxilla, its sutural areas with that bone matching exactly. This element is essentially com-

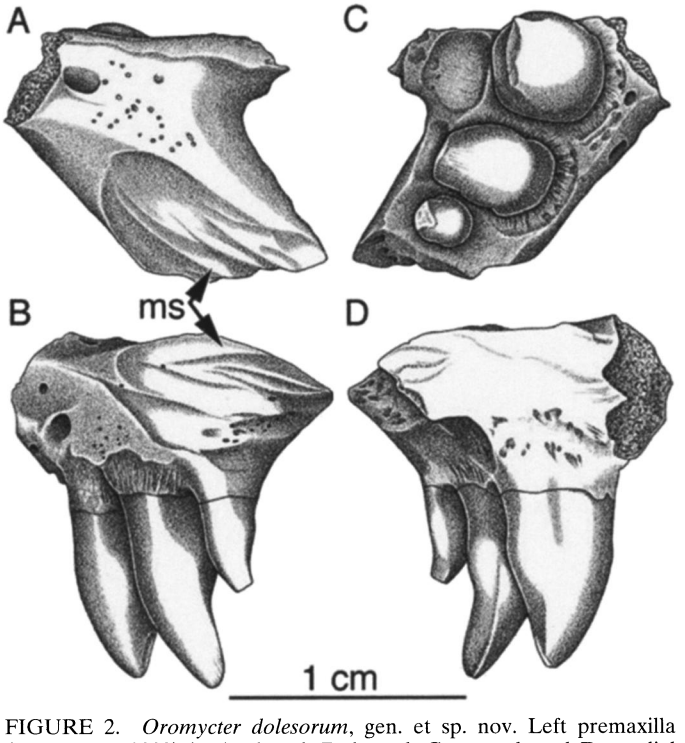

FIGURE 2. *Oromycter dolesorum*, gen. et sp. nov. Left premaxilla (FMNH PR 2283) in **A**, dorsal; **B**, lateral; **C**, ventral; and **D**, medial views. Scale bar equals 1 cm. **Abbreviation**: **ms**, maxillary suture.

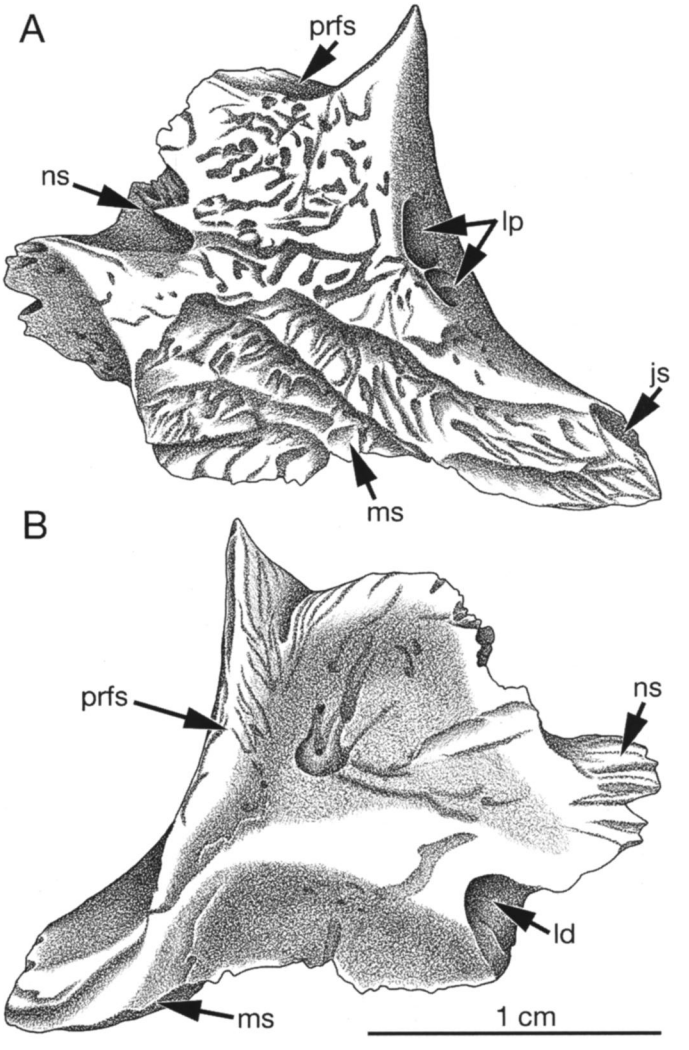

FIGURE 3. *Oromycter dolesorum*, gen. et sp. nov. Left lacrimal (FMNH PR2285) in **A**, lateral, and **B**, medial views. Scale = 1 cm. **Abbreviations**: **js**, jugal suture; **ld**, lacrimal duct; **lp**, lacrimal pucti; **ms**, maxillary suture; **ns**, nasal suture; **prfs**, prefrontal suture.

plete, and shows several clearly caseid features. As in other caseids, this element is short and tall, but this shortness is not related to its exclusion from the narial opening, but rather the reduced distance between the naris and the orbit. Its height is related to the typical caseid dorsoventral enlargement of the narial opening. Along its posterior edge, there is a tall, transversely wide orbital shelf that formed most of the anterior edge of the orbit, and carries a pair of openings for the lacrimal duct. The anterior opening of the lacrimal duct can also be determined because of the isolated nature and completeness of this bone. It opens into the area of the external naris, just in front of the anterodorsal process of the maxilla. This opening can be seen as a strongly depressed area with a rounded medial edge along the anteroventral corner of the bone.

The sutural surface with the maxilla is very large, occupying nearly one third of the lacrimal bone in lateral view. This surface that underlies the large anterodorsal process of the maxilla is complex, with large ridges and grooves. A small, posteriorly directed indentation marks the contact with the jugal. The lateral surface of the bone dorsal to the maxillary suture is strongly sculptured, and the pattern of this ornamentation is similar to that in other caseids where this area is known. Anteriorly the lacrimal has a particularly complex structure, with a large interdigitating suture with the nasal that extends anteroventrally to the level of the superior lacrimal foramen, and a narial shelf that overlies a ventral process of the nasal and contributes to the typical caseid external narial shelf. The dorsal edge of the lacrimal forms a sutural area with the prefrontal, but a large medial sutural area indicates that a process of the prefrontal extended ventrally along the medial surface of the lacrimal. However, the ventral extent of the prefrontal cannot be determined precisely.

This bone, although clearly belonging to a caseid, shows some features that are more primitive than in any other member of this clade. Most significantly it is relatively longer than in other caseids, with a significantly larger and longer lateral surface than in all other members. In addition, although there is a distinct, caseid lacrimal contribution to the external narial shelf, this area of the bone is not as well developed as in other caseids, and there is no anterior thickening of the bone in the area of the narial shelf. These two features indicate that in *Oromycter* the external naris was probably not as large as in other caseids, and the external narial shelf was not as extensive.

Dentary—The dentary (Fig. 4) is represented only by two incomplete elements, but the available evidence indicates that the mandibular symphysis was large, and as in other caseids, the splenial contributed extensively to it. The anterior dentary fragment is pierced by numerous foramina medially along its meckelian groove, just above the sutural surface for the splenial bone. The first foramen is directed medially, whereas the others have posteriorly directed grooves running along the dentary bone. These foramina are probably connected to numerous external dentary foramina. The latter are directed laterally at the level of the third and fourth dentary teeth, but two large foramina that open laterally at the level of the first and second tooth have anteriorly directed superficial grooves. The height of the dentary in its mid-portion is preserved on the second dentary fragment, and is greater than in other, younger caseids. The posterior dentary fragment also indicates that this bone had a well-developed medial sutural surface with the splenial along the alveolar shelf, and a strongly interdigitating sutural contact with the coronoid bone posterior to the tooth row. It is difficult to determine if there was one or two coronoids in this caseid.

Although the first dentary tooth is damaged and appears to be in the process of replacement, its basal diameter is larger than those of the others in the series. The second dentary tooth is complete and is the largest in the preserved series, indicating that the first two teeth are procumbent. The labial surface of the second tooth has an oval wear surface where an opposing maxillary tooth must have made contact with it. As in the premaxillary and maxillary dentition, there is extensive bone of attachment that extends onto the teeth, well above the dentary bone proper. In addition, there are three clearly marked, shallow resorption pits lingually, one at the level of the second tooth on the anterior fragments and two additional pits on the posterior fragment.

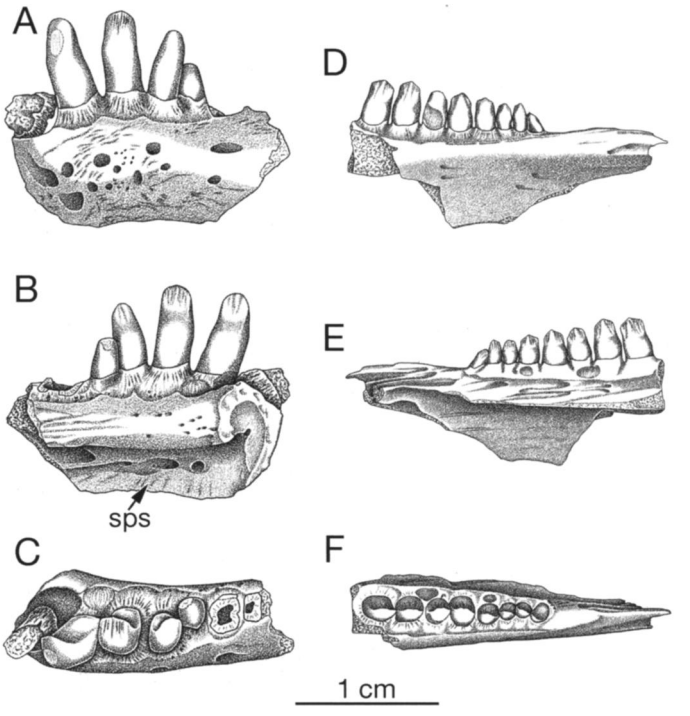

FIGURE 4. *Oromycter dolesorum*, gen. et sp. nov. **A–C,** anterior left dentary fragment (FMNH PR2286) in lateral, medial, and occlusal views; **D–F**, posterior left dentary fragment (FMNH PR 2287) in lateral, medial, and occlusal views. Scale bar equals 1 cm. **Abbreviation**: **sps**, splenial suture.

Dentition

The marginal dentition, preserved on the premaxilla, maxilla, and dentary (Figs. 1, 2, 4), is characterized by a number of caseid features. There is extensive bone of attachment that extends apically from the bone proper onto the wall of each tooth. This bone of attachment extends all around the base of each tooth, and is well developed both lingually and labially. In contrast to most other synapsid dentitions, the most significant dental curvature is lingually oriented, rather than distally (or posteriorly). Although some caseids have both lingual and distal components to their dental curvature, in all known caseids the lingual curvature is greater. Associated with this lingual curvature is a distinct lingual shoulder that separates the more blade-like apical portion of the tooth from the broader, rounded base. The teeth also show a broadly curving, convex labial surface, giving the dentition a transversely broad appearance. As in other caseids, the mesio-distally broad, spatulate, apical end is lined up with the general outline of the jaw margin, creating a marginal cutting edge along the dental series. However, all teeth of *Oromycter* lack the typical leafy serrations that characterize other caseids. These serrations range from three in *Cotylorhynchus* to more than ten in *Casea rutena* and in *Ennatosaurus.* Instead, the spatulate apical portion of each tooth is supported by a midline ridge, where the tooth forms a modest apex, and on either side of this

ridged apex, the cutting edge has a roughened edge, almost like tiny serrations.

Postcranial Elements

Two additional types of postcranial elements can be assigned with some confidence to the Dolese caseid: anterior caudal vertebrae and phalanges (Fig. 5). The caudal vertebrae have a massive centrum with a wide, rounded, ventral surface, large, wide areas of articulation between centra, and broad areas of articulation with hemal arches ventrally. These morphological features are entirely consistent with caseid caudal vertebrae. In addition, as in other caseids, the zygapophyses are large and retain large surfaces of articulation, while the neural spine is narrow and slender (Fig. 5A).

Caseid phalangeal elements are immediately recognizable because of their short, stubby configuration and large proximal and distal ends. More significantly, caseid phalanges are characterized by the unique morphology of their interphalangeal surfaces of articulation (Fig. 5B–D). They are not perpendicular to the long axis of the phalanx, as in other basal amniotes, but are strongly tilted to create large surfaces that are facing both proximally and ventrally on the larger head of the phalanx (Fig. 5C) and anteriorly almost entirely dorsally on the smaller distal expansion (Fig. 5D). The terminal or ungual phalanx is also unique in its morphology, characterized by the presence of a massive retractor process ventrally (Fig. 5E, F), and a broad, spatulate, distal expansion that is separated from the distinctly narrower dorsal surface of the bone by two well-developed grooves that extend from the level of the retractor process to the tip of the phalanx (Fig. 5F, G).

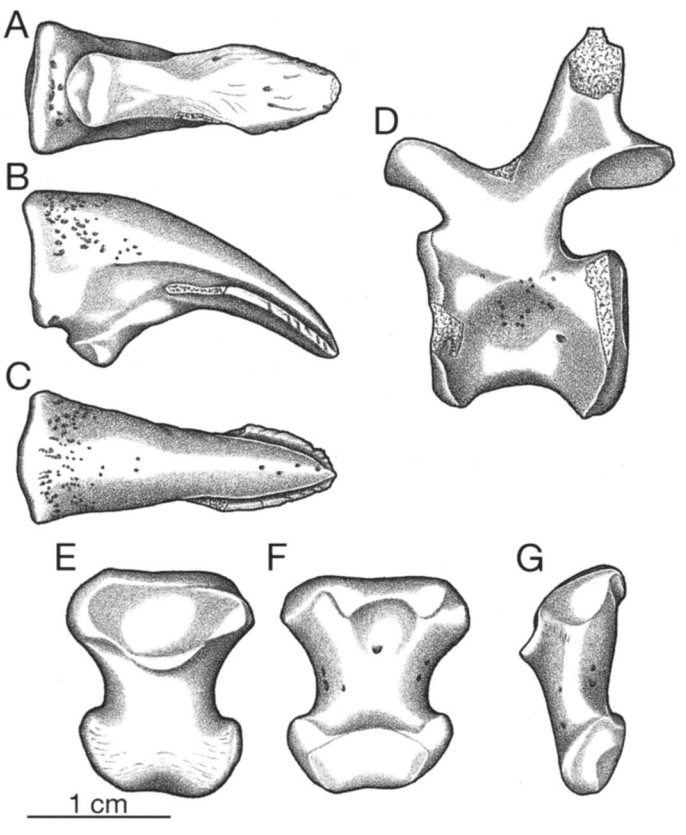

FIGURE 5. *Oromycter dolesorum*, gen. et sp. nov. **A–C**, ungual phalanx (FMNH PR 2289) in ventral, lateral and dorsal views; **D**, mid-caudal vertebra (FMNH PR2290) in lateral view; **E–F**, phalanx (FMNH PR 2288) in dorsal, ventral, and lateral views. Scale bars equal 1 cm.

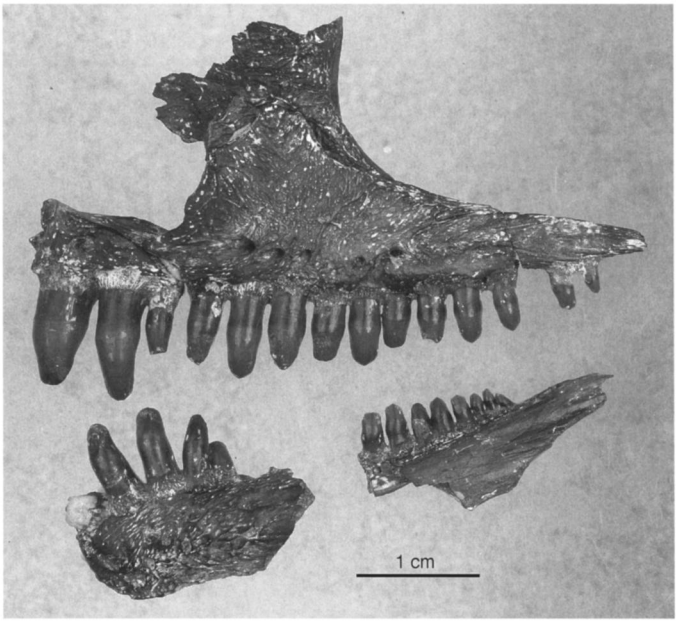

FIGURE 6. *Oromycter dolesorum*, gen. et sp. nov. Skull elements from the left side of the face, reattached along sutural surfaces, and with the dentary fragments in the approximate correct position relative to the upper tooth row. Scale bar equals 1 cm.

DISCUSSION

The Dolese fossil assemblage is characterized by the presence of thousands of apparently isolated skeletal elements, and the occasional preservation of associated or articulated remains. The caseid cranial material described here appears to represent the remains of a single individual, but this interpretation is tentative, given the overwhelming number of isolated elements found in this locality.

There is little doubt that the skeletal remains assigned to *Oromycter* represent a caseid. Although the remains are fragmentary, the preserved elements show an impressive number of caseasaur (1) and caseid (2) autapomorphies:

(1) As in all caseasaurs, the premaxilla has a distinct rostral process formed by the nasal process of the bone. The orientation of the teeth relative to the maxillary bone also indicates that the lateral surface of the maxilla was not vertical, but was tilted so that it would have been visible in ventral view. The morphology of the lacrimal indicates that an external narial shelf was present, even though the nasal bone is not preserved.

(2) As in all caseids, the dentition lacks a caniniform region or caniniform teeth, and the anterior premaxillary teeth are the largest of the marginal series. The teeth are spatulate, with distinct lingual shoulders, and their spatulate tips are gently curved lingually rather than posteriorly. The maxilla has a well-developed, anteriorly tilted, dorsal process, and a series of marginal foramina that are arranged along the length of the bone, just above the level of the alveolar shelf. The overall morphology of the lacrimal bone, its external pattern of sculpturing, its reduced length and anterior narial emargination are also typical for caseids. Similarly, the external pattern of sculpturing on the dentary, the distinct procumbent anterior dentition on the dentary, and the presence of the largest marginal tooth at the front of the dentary series are also caseid features.

Postcranially, there are clearly caseasaur or caseid features in the phalangeal elements, in particular the presence of strongly concave and convex surfaces of articulation, respectively, and strongly tilted surfaces for increased overlap. However, in the absence of eothyridid postcrania, it is not possible to determine if these features are caseasaur or caseid autapomorphies.

In accordance with the age of *Oromycter,* there are several cranial features that represent the primitive condition for caseids. There is a larger number of marginal teeth than in other caseids of similar size; the teeth lack the distinct leafy serrations that are characteristically found along the spatulate edge; and perhaps most strikingly, the lacrimal and maxillary bones, although showing several caseid features, are nevertheless longer than in other caseids, and lack anteriorly the massive medial shelf that otherwise forms the posterior edge of the naris. The phylogeny of caseid synapsids is poorly known, and a revision and phylogenetic analysis of the group is in progress. The available osteological evidence provides clear evidence that *Oromycter* is the sister taxon of all other described caseids, and is more closely related to *Casea* and *Cotylorhynchus* than to *Eothyris.*

CONCLUSIONS

Caseids are a particularly important group of synapsids for the following reasons: (1) all known members of this clade show adaptations to a herbivorous diet (Reisz and Sues, 2000); (2) some of the later members of this group become the largest known terrestrial vertebrates of their time; (3) this group of highly autapomorphic amniotes extends well into the Middle Permian, and its members have been found in Late Kazanian/Early Tatarian sediments in Russia; (4) the history of caseids is characterized by a particularly long ghost lineage that extends through much of the Early Permian, followed by strong diversification that extends beyond the so-called more progressive Permo-Carboniferous synapsids.

The importance of *Oromycter* lies in its age and basal position within caseids. If the estimated age of the Dolese quarry is correct, we have here the oldest known member of this clade of early herbivores. Dolese preserves a rich, varied faunal assemblage that includes exclusively terrestrial forms in a unique depositional setting that has been interpreted as an upland depositional regime (Sullivan and Reisz, 2000). The discovery of this basal caseid in an upland depositional environment provides support for the hypothesis that the initial evolutionary history of this group is unknown because these early caseids lived in areas away from the common depositional environments of the Early Permian. A recent discovery of a caseid in the Early Permian of Germany (pers. obs.), in the upland deposits of Bromacker, provides added support for this hypothesis. It appears that only after considerable time were caseids able to invade successfully the lowland, deltaic, flood-plain environments that are so richly recorded in the Permo-Carboniferous sediments North America and Europe. This apparent invasion seems to coincide with the disappearance of another group of herbivorous synapsids, the edaphosaurids.

This raises the possibility that these two groups of herbivorous synapsids represent an example of competitive exclusion during the earliest known history of terrestrial herbivory among vertebrates. It is not possible to determine precisely at what level the competitive exclusion worked between edaphosaurids and caseids, but the scant evidence suggests that it is more plausible that edaphosaurids became extinct, freeing the ecospace that they occupied, followed by the caseid colonization. If there were any direct competition between the two forms, we would expect to see the two forms coexisting, but that is not the case. Similarly, caseids may have been replaced in the Upper Permian by the herbivorous pareiasaurs, a group of large parareptiles that also had spatulate dentition with large leafy serrations and no dental occlusion.

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