ment for this specimen. I am indebted to Dr. Frank Carpenter of Harvard University for his help and comments in the taxonomic placement of this fossil.

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MANUSCRIPT RECEIVED JANUARY 3, 1978
REVISED MANUSCRIPT RECEIVED SEPTEMBER 16, 1978

DENTAL ANOMALY IN THE EARLY EOCENE CONDYLARTH *ECTOCION*

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Dental anomalies are not common in the mammalian fossil record, and few cases have been reported in the paleontological literature. The most frequently observed abnormalities include supernumerary teeth, usually at the back of the molar series or in the premolar series, and hypodontia or absence of teeth (Wilson, 1955; McKenna, 1960; Archer, 1975; Wang and Wu, 1976; Mellett, 1977). Such oddities are better known in Recent mammals (e.g., Archer, 1975, and references cited therein), particularly humans, for which there exists an extensive literature in the annals of human dental pathology. We record here a very curious dental anomaly of a type, to our knowledge, not previously mentioned in paleontological reports.

Since 1975, thousands of specimens of late Paleocene and early Eocene mammals have been recovered by University of Michigan Museum of Paleontology (UM) expeditions to the Clark's Fork Basin, northern Bighorn Basin, Wyoming. These include more than 500 jaws and hundreds of isolated teeth of the phenacodontid condylarth *Ectocion*. In 1977, the junior author collected an unusual specimen of *Ectocion osbornianus*, UM 69450, at UM Locality SC-207 (Willwood Formation, early Eocene, lower "Gray Bull beds" of early Wasatchian age). This is the only mammalian fossil in the entire collection that preserves a striking anomaly. UM 69450 consists of partial right and left lower dentitions including right P_{3-4} and M_{1-3} and left P_{3-4} and M_3. Both right

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TEXT-FIG. *1*—Lower teeth of *Ectocion osbornianus*. *A*, buccal and *B*, lingual views of the left anomalous P_3, UM 69450. *C*, lingual *D*, crown and *E*, buccal views of the right anomalous P_{3-4} and normal M_1, UM 69450. *F*, buccal view of normal right P_{3-4}–M_1, UM 65382. Spacing and orientation of teeth in *C*–*E*, including relatively low P_3 and elevated P_4, are due to postmortem distortion. Crown of right P_3 (*C*) is divided almost to base; enamel was originally continuous around the base but appears discontinuous due to breakage.

JOURNAL OF PALEONTOLOGY, V. 53, NO. 3, MAY 1979
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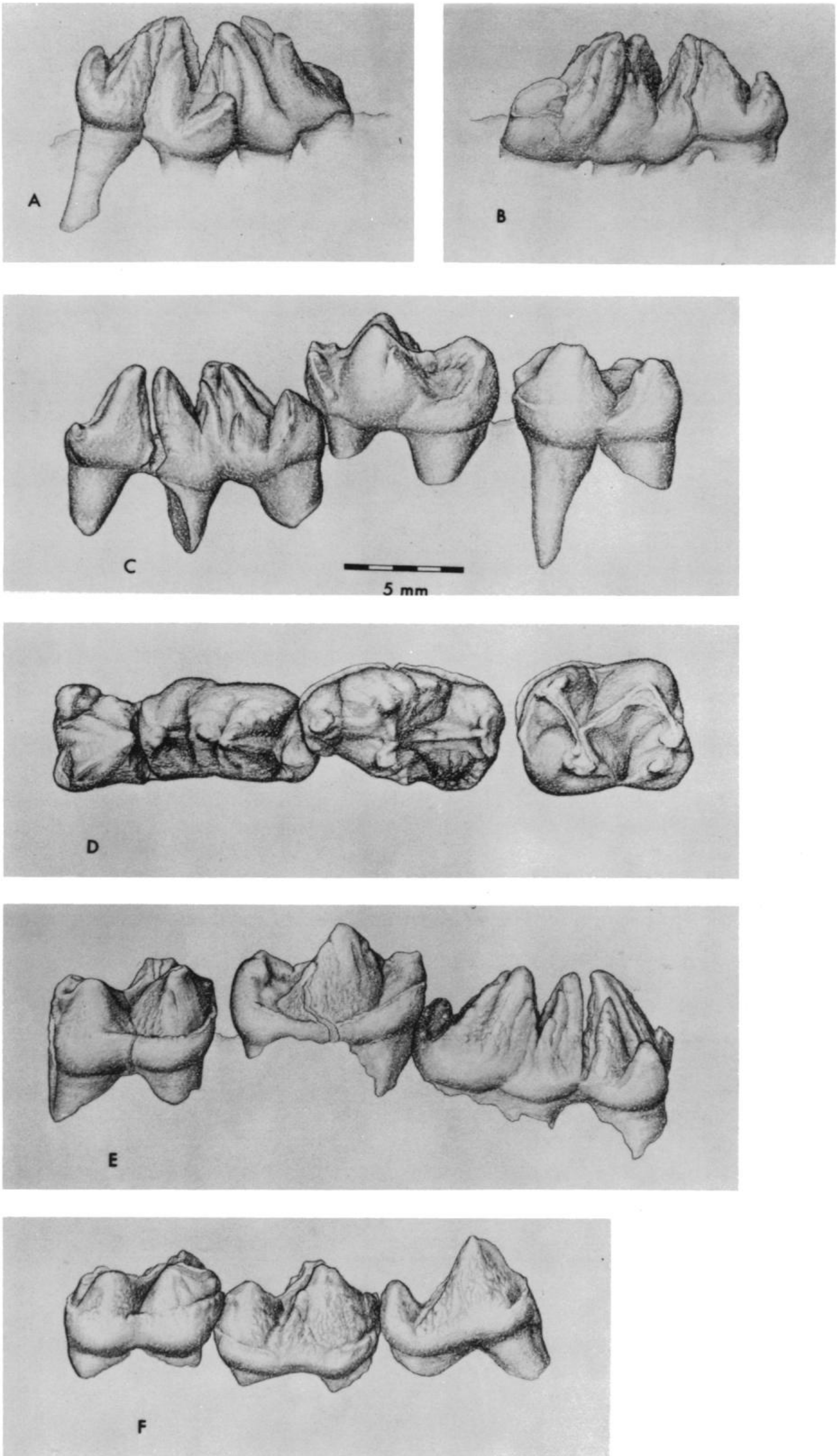

A
B
C
5 mm
D
E
F

and left P_3 are severely malformed. The fourth premolars also are atypical, though not nearly to the degree as the third premolars. The molars are structurally normal.

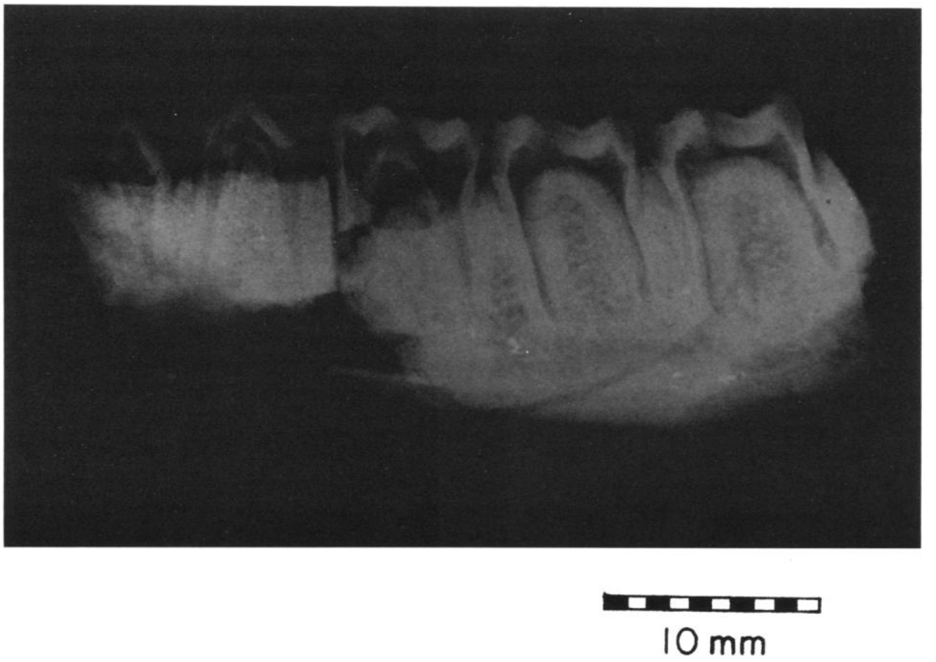
The lower P_4 in normal *Ectocion* (Text-fig. 1F) is rather variable in morphology. Typically it is submolariform, differing from the molars in being narrower and having a more anteroposteriorly extended trigonid and narrower talonid. It has a low paraconid shelf directed more anteriorly than in the molars, and the paraconid is weak or absent. The talonid is basined, with the entoconid usually well developed (West, 1976) and a distinct hypoconulid sometimes present. In UM 69450 (Text-fig. 1C–E), P_4 has a long trigonid with a very prominent paraconid. The hypoconid is high, but the postcristid slopes lingually with no indication of either entoconid or hypoconulid; hence the talonid is not basined.

The lower P_3 in typical *Ectocion* is a simple tooth with a high protoconid, very small paraconid and metaconid variably present, and a single low talonid cusp (Text-fig. 1F). The third premolars in UM 69450 (Text-fig. 1A–E) are elongate, multicusped anomalies. Although the left and right P_3s are similarly deformed, they are not exact mirror images. The cusp homologies are unclear, for at least two cusps resemble a protoconid, and each of these appears to be twinned. The left P_3 has four roots and the right P_3 at least three and possibly four; the precise number is difficult to ascertain because of postmortem fracturing of the mandible. Due to this breakage and to its density, radiographs of the fossil also failed to clarify the root configuration of the right P_3.

To some extent the premolars resemble deciduous teeth of *Ectocion,* but several features confirm that they are deformed permanent teeth. They are neither lighter in color nor lower crowned than the molars, as is often distinctive of deciduous teeth (Simpson, 1951; West, 1971). They are broader than typical milk teeth, and the jaw is deeper and more robust than in juveniles. Deciduous P_4 in normal *Ectocion* is often heavily worn; it is the last deciduous premolar to be replaced and probably the first to erupt (West, 1971). Consequently, it should be more heavily worn than M_1. But UM 69450 exhibits the reverse situation: M_1 is conspicuously more heavily worn than the premolars, and even M_3 (which is fully erupted) shows at least as much wear as the premolars. The fourth premolar is only slightly worn, and P_3 displays almost no wear at all. Finally, radiographs of the specimen did not reveal any teeth within the mandible (but see discussion below). Thus the premolars in UM 69450 can be confidently identified as permanent teeth.

In the human dentition, dental abnormalities generally have been classified on the basis of their morphology. This classification implies, but is not always consistent with their developmental history. Not all anomalies fit into the discrete categories, however, and it is the developmental cause of the anomaly that should be the subject of investigation. Doubled or connate teeth, as in the specimen of *Ectocion* described here, have been termed either geminated, twinned, or fused. Gemination, resulting in a single tooth that usually has a bifid crown, is believed to arise from partial division of one tooth bud (Tannenbaum and Alling, 1963; Levitas, 1965; Pindborg, 1970). The pulp cavity is that of a single tooth. If the geminated tooth is counted as one, the total number of teeth in the affected area is normal. Twinning, or schizodontia, is the presence of two teeth, usually mirror images of each other, interpreted to result from complete cleavage of a single tooth bud (Levitas, 1965). Such a twinned P_2 has been observed in a late Pliocene canid (Fine, 1964). Fusion, or synodontia, applies to teeth joined at the crowns or the roots, or both; the dentine and enamel of both teeth are almost always joined. It is usually said to be a result of union of two or more tooth buds during development, perhaps arising from crowding of tooth primordia (e.g., Pindborg, 1970). According to this interpretation, complete union of the crown and roots, or of only the crowns, will result if fusion occurs early in development of the tooth germs. If it takes place later in development (i.e., after crown formation), the roots alone will be fused (Bier, 1958). However, carpal "fusions" actually result from failure of cartilaginous precursors to separate (Garn et al., 1976), and it has been suggested that "fusion" of teeth also ensues from incomplete division of the dental lamina into separate tooth germs (Hitchin and Morris, 1966).

Fusion may be unilateral or bilateral. In humans, it is most frequent in the deciduous incisors (Clayton, 1956; Bier, 1958), but it has also been observed in deciduous lower pre-



TEXT-FIG. *2*—Radiograph of right mandible of juvenile *Ectocion osbornianus,* UM 65558, with dP_2–dP_4, $M_{1\text{-}2}$. Anterior border of M_3 alveolus indicates that M_3 was at least partially erupted. Roots of deciduous premolars have not been resorbed and there is no indication of permanent premolar calcification within the jaw.

molars (Grahnén and Granath, 1961), supernumerary premolars (Shapira, 1974), and in permanent incisors and second and third molars (Tannenbaum and Alling, 1963). Archer (1975), in a thorough study of dental abnormalities in marsupials, observed fusion only in the premolar series. If the fused teeth are counted as one, the number of teeth in the affected area is always less than normal.

The term "fusion," deriving from the ultimate morphology of the tooth but not necessarily indicative of its early development, may therefore be a misnomer. Hitchin and Morris (1966) advocate the term connation, which makes no implication about developmental history.

The complex crown of P_3 in UM 69450 is completely united (Text-fig. 1A–E), but appears to incorporate at least two teeth. This inference may also be drawn from the presence of more than two roots. These features suggest that the anomaly arose through fusion (or incomplete separation) of two tooth germs—either those of P_2 and P_3, or perhaps of P_3 and a supernumerary premolar—probably early in development of the premolar anlagen. Nonetheless, the crown is larger and more complex than would be expected from this event alone. The apparent twinning of some of the cusps suggests that gemination may also be involved, i.e., that the developing tooth buds underwent partial division. The ultimate cause of such abnormalities is not known, but many factors have been proposed, for example disease, trauma, and crowding. Many dental anomalies are probably not genetically controlled, but there is some evidence that bilateral anomalies may be related to dental morphogenetic fields (Archer, 1975).

During the course of this study, we examined a number of juvenile specimens of *Ectocion* preserving deciduous teeth. Radiographs of some of them indicate that permanent premolars in *Ectocion* may calcify at a relatively later stage than in many other mammals. For example, even in some individuals of *Ectocion* in which M_3 is partially erupted, the deciduous premolars are still functional and there is little or no evidence of permanent tooth formation within the jaw (Text-fig. 2; see also West, 1971: fig. 2). A similar situation can be found in the Oligocene insectivore *Leptictis acutidens* (West, 1972), in which molars erupted before significant wear occurred on deciduous premolars. In some mammals, however, nearly fully formed permanent premolars lie within the jaw while deciduous premolars are still functional and some molars have not yet erupted (see, e.g., Garn and Lewis, 1963: fig. 1; Rose, 1973: fig. 5; Mellett, 1977: fig. 52). Sequences of calcification and eruption vary considerably both between species and intraspecifically, and the sequence of development is not always the same as that of eruption (Garn et al., 1956; Slaughter et al., 1974; Schwartz, 1975). Hence it is not surprising that UM 69450 and other individuals of comparable age have functional permanent premolars, whereas in apparently only slightly younger individuals the permanent premolars have hardly begun to calcify.

ACKNOWLEDGMENTS

We are indebted to Dr. P. D. Gingerich (UM) for permission to describe this unusual specimen. Professors S. M. Garn and A. R. Burdi of the Center for Human Growth and Development, University of Michigan, helped to clarify several points regarding dental development. Drs. Garn and Gingerich and Mr. D. W. Krause provided helpful criticisms of the manuscript. Text-figure 1 was skillfully drawn by Ms. Karen Payne, and the radiographs, including Text-figure 2, were prepared by Professor A. G. Richards of the University of Michigan School of Dentistry. Ms. Karna Steelquist assisted with photography. To all of them we extend our appreciation. This research was supported in part by NSF Grant DEB 77-13465 to Dr. P. D. Gingerich.

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MANUSCRIPT RECEIVED MAY 19, 1978

REVISED MANUSCRIPT RECEIVED SEPTEMBER 12, 1978