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FIRST EVIDENCE OF THE ZYGOMASSETERIC STRUCTURE OF *DIPLOLPHUS* TROXELL, 1923, (MAMMALIA, RODENTIA) AND ITS SYSTEMATIC IMPLICATIONS

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ABSTRACT

The systematics (familial and suprafamilial allocation) of the Oligocene rodent *Diplolophus* Troxell, 1923, has long been in question pending the description of the zygomassteric structure of the maxilla. Two partial maxillae of this rodent retain a portion of the base of the zygomatic arch and partial palatine bone. The portions of the maxilla that are preserved suggest a dipodoid-like zygomassteric structure most similar to that of late Eocene rodent *Nonomys* Emry and Dawson, 1973. This morphology supports the alliance of *Diplolophus* with other early, dipodoid-like rodents.

INTRODUCTION

Diplolophus insolens, Troxell, 1923, is an enigmatic rodent from the Orellan (early Oligocene) of the Great Plains that is distinct in possessing the dental formula of a muroid rodent (I1/i1, M1-3/m1-3) but attaining the occlusal dental morphology of a geomyoid (six-cusped, bilophate molars). The systematics of this genus has long been debated, and it has been referred to the Geomyoidea, Dipodoidea, or Muroidea by various authors (see Korth, 1994; Walsh, 2010, for summaries). Most recently, Walsh (2010) has reviewed the taxonomic history of *Diplolophus* and suggested that it was most closely related to the late Eocene *Nonomys* Emry and Dawson, 1973, due to the similarity in the dental formula and the recognition of a specimen intermediate in the occlusal morphology of the cheek teeth between *Nonomys* and *Diplolophus*. Walsh (2010) concluded that both of these genera could not be included with confidence in any recognized family, and placed them in "Infraorder Myodonta *incertae sedis*." Several authors have noted that the assignment of *Diplolophus* to a family might be resolved if the zygomasseteric structure were known (Korth, 1994; Emry, 1981; Walsh, 2010). Two specimens of *Diplolophus* consist of a maxilla that retains the base of the zygomatic arch and partial palatine. These specimens are the basis for this study and suggest the probable systematics of the genus.

Dental nomenclature follows that of Wood and Wilson (1936). Upper teeth are designated by capital letters, lower teeth by lower-case letters (e.g. M1 or m1). Abbreviations for institutions: FMNH, Field Museum of Natural History; UNSM, University of Nebraska State Museum; YPM, Yale Peabody Museum. Measurements were taken to the nearest 0.01 mm.

SYSTEMATIC PALEONTOLOGY

Diplolophus Troxell, 1923
Diplolophus insolens Troxell, 1923
Gidleumys adspectuans Wood, 1936

Type Specimen—YPM 10368, right dentary with m1-m3.

Specimens Examined—FMNH P 25875, right maxillary fragment with M1-M2; UNSM 66194, left maxillary fragment with M1-M3 (Specimen listed and figured by Barbour and Stout [1939:figs. 13, 14E] as N.S.M. 9-5-7-36 SP).

Horizon and Locality—Holotype from uncertain locality, possibly Orellan Cedar Creek Member, White River Formation, northeastern Colorado (Barbour and Stout, 1939); specimens described here are from Orella Member, Brule Formation, White River Group, Sioux County, Nebraska. FMNH specimen from locality cited as "NE of Harrison" (museum records). UNSM specimen is from UNSM locality Sx-16, "…near top of badlands escarpment to the east of Toadstool park, northwest of Crawford, Nebraska…." (Barbour and Stout, 1939:32).

Description—The dentition of *Diplolophus* has been described in detail by Barbour and Stout (1939:fig. 14E) including the UNSM specimen discussed herein. FMNH 25875 is the same size and morphology as the previously described material, and clearly referable to *D. insolens* (Figure 1A, E).

FMNH P 25875: The molars are contained within a piece of the maxilla that extends posteriorly to the anterior alveolus for M3. The dorsal surface of the maxilla above the molars is preserved along with the base of the zygomatic arch on the anterolateral side. There is a

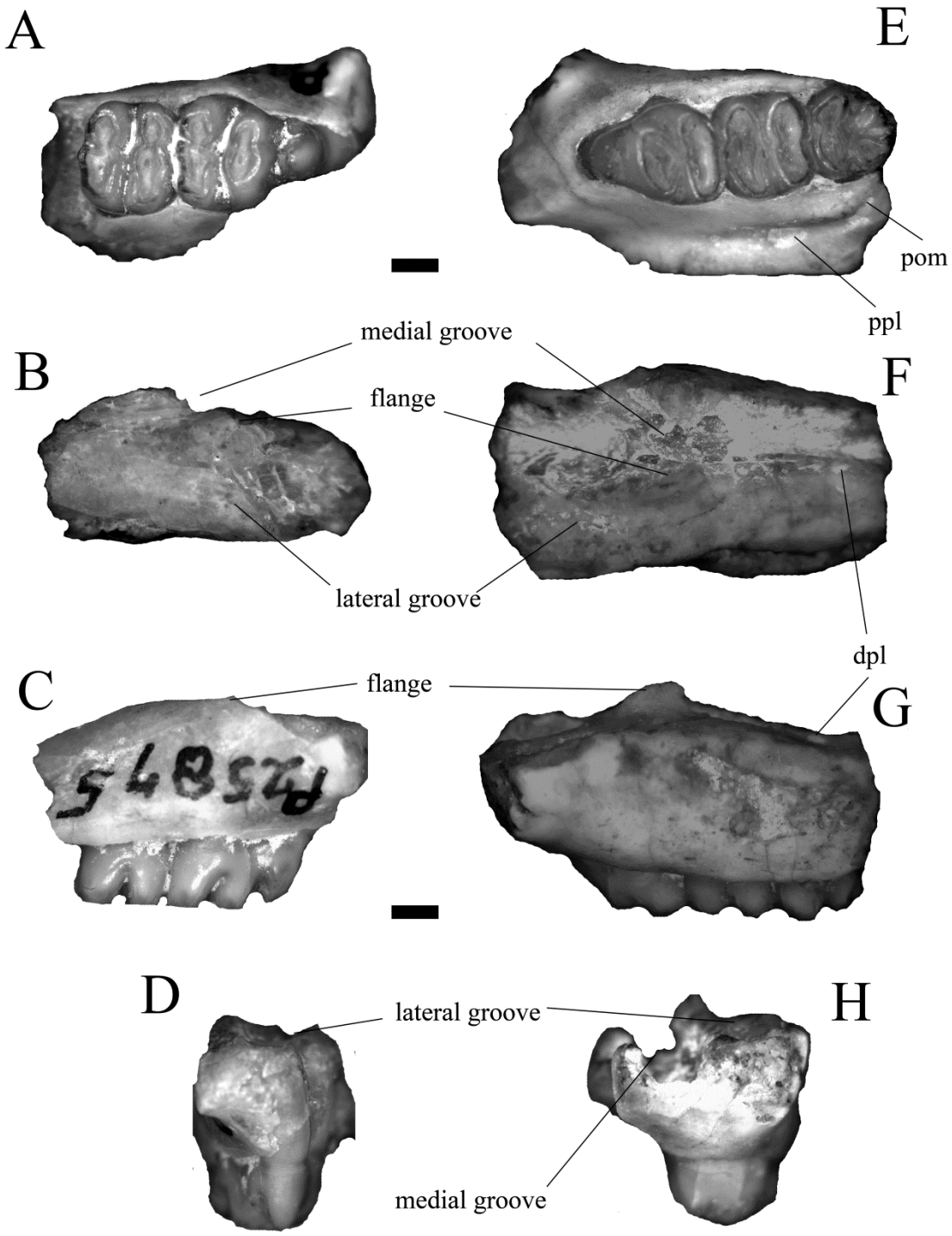

FIGURE 1. Fragmentary maxillae and dentition of *Diplolophus insolens*. A-D, FMNH 25875, A, ventral (occlusal view, M1-M2). B, dorsal view. C, lateral view. D, anterior view (occlusal surface toward bottom of page). E-H, UNSM 66149. E, ventral (occlusal view, M1-M3). F, dorsal view. G, lateral view. H, anterior view (occlusal surface toward bottom of page). Anterior to the right on A-C; to left on E-H. Bar scale = 1 mm.

TABLE 1. Dental measurements of *Diplolophus insolens*. Measurements of additional referred specimens compiled with those taken from Barbour and Stout (1939:table 1). Abbreviations: L, anteroposterior length; W, transverse width; N, number of specimens; M, mean; OR, observed range; SD, standard deviation; CV, coefficient of variation. Measurements in mm.

	LM1	WM1	LM2	WM2	LM3	WM3
N	5	5	3	3	1	1
M	3.28	2.62	2.18	2.68	2.20	2.45
OR	3.00–3.60	2.50–2.75	2.13–2.25	2.60–2.80		
SD	0.26	0.11	0.06	0.11		
CV	7.84	4.33	2.95	4.03		

	Lm1	Wm1	Lm2	wm2	Lm3	Wm3
N	6	6	6	6	5	5
M	2.43	2.37	2.10	2.64	2.56	2.45
OR	2.30–2.50	2.30–2.45	1.95–2.25	2.60-2.75	2.50–2.60	2.40–2.50
SD	0.10	0.07	0.11	0.06	0.05	0.05
CV	4.07	2.89	5.47	2.21	2.14	2.04

small sliver of the palatine bone along the medial side of the maxilla extending from the posterior extent of the bone to the level of the posterior root of M1. Dorsally, there is a distinct groove that extends the entire length of the maxilla along the dorsal surface. It is narrowest and deepest dorsal to the posterior root of M1. The anterior opening is visible in an anterior view of the maxilla. Only the ventral border of the foramen that leads to this groove is preserved. The maximum anterior width of the opening that can be measured is approximately 0.9 mm. On the anterior-most dorsal part of the preserved maxilla is the base of the zygomatic arch. It extends laterally away from the tooth row to a small point. It originates lateral to the anterior extent of the anterocone of M1. There is no evidence of any kind of modification such as anterior tilting or muscular attachment.

UNSM 66194: This specimen retains more of the maxilla anterior to the cheek teeth as well as a larger portion of the palatine medially, and a tiny fragment of the palatine dorsal to the maxilla at the base of the orbital wall. Ventrally, the palatine extends anteriorly to a point even with the center of M1. A relatively large, oval posterior maxillary foramen is entirely within the palatine, even with the center of M2. Medial to M3 the maxilla extends ventrally below the level of the palatine, forming a small shelf that overhangs the palatine and maxillary-palatine suture. Within the small pocket formed between the palatine and maxillary is the posterior maxillary foramen. Anterior to M1 is a small flattened area of bone that appears to be for the attachment of the masseter muscle. There is no indication of tilting or expansion of the attachment of the muscle as might be expected in a sciuromorphous or myomorphous zygomasseteric structure.

On the dorsal surface of the maxilla, just above M3 is a small portion of the palatine that contains the maxillary-palatine suture and a small dorsal palatine foramen. A shallow groove runs anteriorly along the dorsal side of the maxilla as in FMNH P 25875. It is constricted near the center of its length (dorsal to the posterior margin of M1), also as in FMNH P 25875. However, UNSM 66149 is more complete and on either side of the constricted area the bone forms a thin flange on the lateral side and a small knob on the lingual side. Both of these structures are broken dorsally. Anterior to this, the canal deepens due to some breakage but ultimately opens anteriorly. The anterior exit of the canal is broken away, so the exact size and shape of a foramen cannot be determined. Lateral to the lateral bony flange is another shallow groove that runs anteriorly, and also opens anteriorly lateral to, and slightly more dorsally than the medial groove. This lateral groove is not preserved on FMNH P 25875 because the area of bone is not preserved. The lateral groove is interpreted as the base of the canal for the masseter muscle that passes through the infraorbital foramen. The medial groove is interpreted as the canal leading to the neurovascular infraorbital foramen.

Discussion—The dentition of FMNH P 25875 is indistinguishable in size and morphology from that of *Diplolophus insolens* figured and described elsewhere (Troxell, 1923; Wood, 1937; Barbour and Stout, 1939; Korth, 1994) and is thus referable to this species. Its occurrence in the Orellan is also consistent with that of

this species. Flynn (2008) listed *Diplolpohus* as occurring earlier, but this was based on specimens that were later referred elsewhere (Walsh, 2010). UNSM 66194 has already been identified as *D. insolens* by Barbour and Stout (1939).

CONCLUSIONS

The small portion of the zygomasseteric structure of *Diplolophus* that is preserved on FMNH 25875 and UNSM 66149 is only fragmentary, but preserves enough of the base of the zygomatic arch and anterior foramina to suggest a probable zygomasseteric structure. The two recognizable grooves on the dorsal surface of the maxilla suggest the presence of two foramina. The medial grove and its anterior opening of the foramen are interpreted as a secondary neurovascular foramen and the medial groove as that for the infraorbital foramen that contains the masseter muscle. This morphology, along with the anterior extent of the palatine and lack of modification of the anterior root of the zygomatic arch, suggests that the structure was similar to that of dipodoid rodents that are hystricomorphous with a secondary, smaller foramen ventral to the infraorbital foramen. This type of structure, along with the reduced dental formula, is also present in the Chadronian *Nonomys* and Uintan to Duchesnean *Simimys* Wilson, 1935 (most closely approaching that of *Nonomys* [Emry, 1981:figs. 3, 4]).

The systematics of *Diplolophus* are still uncertain, but it appears that it belongs to a group that includes *Nonomys* and possibly *Simimys*. The apparent zygomatic structure of *Diplolophus* excludes it from the Geomyoidea that have a sciruomorphous zygomasseteric structure and a more anteriorly positioned infraorbital foramen. The small neurovascular foramen also excludes *Diplolophus* from the Muroidea that have a myomorphous zygomasseteric structure (anterodorsally tilted zygomatic plate and much higher infraorbital foramen) and lack the accessory foramen.

Diplolophus and *Nonomys* have been included in the subfamily Nonomyinae (Walsh, 2010) but not formally included in any family. The dental similarity between these two genera (Korth, 1994; Walsh, 2010), along with the similarity in the zygomasseteric structure, supports this grouping. The inclusion of *Simimys* with these genera is less likely due to the marked differences in the occlusal morphology of the molars of the latter (even though it has the same dental formula) and attains the dipodoid-like zygomatic structure (Wilson, 1935; Lillegraven and Wilson, 1975; Walsh, 2010). In all, the cladogram presented by Walsh (2010:fig. 9) that suggests a relationship of Nonomyinae with dipodoids and muroids is supported by the specimens described above.

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