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PARTIAL SKULL OF THE PLESIADAPIFORM PRIMATE *IGNACIUS* FROM THE EARLY EOCENE OF WYOMING

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Kenneth D. Rose and Philip D. Gingerich

Abstract.— A new partial skull of the plesiadapiform primate *Ignacius* (Paromomyidae) is described. It consists of the anterior half of the skull, preserving the rostrum and palatal dentition essentially intact. This is the first known skull of *Ignacius*, and it is only the sixth skull of a plesiadapiform primate to be found in North America.

The skull is generally similar to that of *Plesiadapis*, but differences in detail indicate that many of the resemblances were acquired independently and reflect similar adaptations rather than common inheritance. Judging from the size of the infraorbital foramen, *Ignacius* appears to have had a well-developed rhinarium and probably facial vibrissae, and its external sensory system was olfaction rather than vision dominated. The skull form suggests that *Ignacius* may have been rather rabbitlike in general adaptation. The premolar number is the most reduced among plesiadapiform primates, and the antemolar dentition contrasts with that of *Phenacolemur*. Hence the new skull further supports the distinctness of *Ignacius* from *Phenacolemur*, and together with other dental remains indicates that the two genera evolved separately but in parallel after the middle Paleocene.

INTRODUCTION

The Plesiadapiformes constitute the first major radiation of the order Primates. They appeared in the latest Cretaceous and reached a peak of diversity and abundance in the middle and late Paleocene, with a few lines continuing well into the Eocene. Some plesiadapiform primates are among the most common elements of North American and European Paleocene faunas. Despite their relative abundance, few are known from more than jaws and teeth. Skulls or partial skulls have been reported from only six of the more than twenty known genera: *Plesiadapis* (Plesiadapidae), *Carpolestes* (Carpolestidae), *Phenacolemur* (Paromomyidae), *Palaechthon* (Microsyopidae), *Cynodontomys* (Microsyopidae), and *Microsyops* (Microsyopidae). Each of these is known from only one or two skulls.

In July, 1975, a field crew from the University of Michigan Museum of Paleontology found the skull of a seventh genus, the paromomyid *Ignacius*, in lower Eocene beds in the northern Bighorn Basin, Wyoming. The specimen consists of the anterior half of the skull, with the rostrum and dentition nearly complete. The back of the skull, the braincase, and the basicranium are not preserved. Although somewhat crushed and deformed, this is one of the best preserved plesiadapiform skulls yet discovered. It provides new information on the cranial morphology of archaic primates, and it also reveals important differences from the closely related *Phenacolemur* that further support recognition of *Ignacius* as a distinct genus.

Abbreviations used herein are as follows: AMNH, American Museum of Natural History, New York; PU, Princeton University Geological Museum, Princeton; UM, University of Michigan Museum of Paleontology, Ann Arbor.

DESCRIPTIVE PALEONTOLOGY

Order PRIMATES

Infraorder PLESIADAPIFORMES

Family Paromomyidae

Ignacius Matthew and Granger, 1921

Type species.— *Ignacius frugivorus* Matthew and Granger, 1921, from the late Paleocene of southern Colorado (Mason Pocket).

Included species.— *Ignacius frugivorus*; *I. fremontensis*, from the late middle or early late Paleocene of Wyoming (Shotgun local fauna); *I. graybullianus*, from the early Eocene of Wyoming (Bighorn Basin); and *I. mcgrewi*, from the late Eocene of Wyoming (Badwater).

Ignacius graybullianus Bown and Rose, 1976

Pl. 1, figs. 1-3; Pl. 2, fig. 2; Text-fig. 1

New material.— UM 65569, anterior half of skull with nearly complete dentition, found by Robert G. Habetler.

Horizon and Locality.— Sand Coulee beds, lower Willwood Formation, lower Eocene (early "Graybullian" sub-age of Wasatchian); UM Locality SC-54, center SE¼, Sec. 26, T 56 N, R 102 W, Park County, Wyoming.

Description.— *Ignacius graybullianus* was recently proposed for about a dozen specimens of a large species of this genus from very early Eocene beds in the central and southern Bighorn Basin. The holotype, a maxilla with P⁴-M², was the most complete known upper dentition, with P³ and M³ each known from a single specimen. The teeth in UM 65569 are larger than those in the holotype, lying at the extreme end of the range or, in several dimensions, exceeding the observed range by about 10%. P³ and M³ also differ in shape from the single examples previously known. Although these differences do not now appear to be statistically significant, they may indicate a specific distinction when better samples are known.

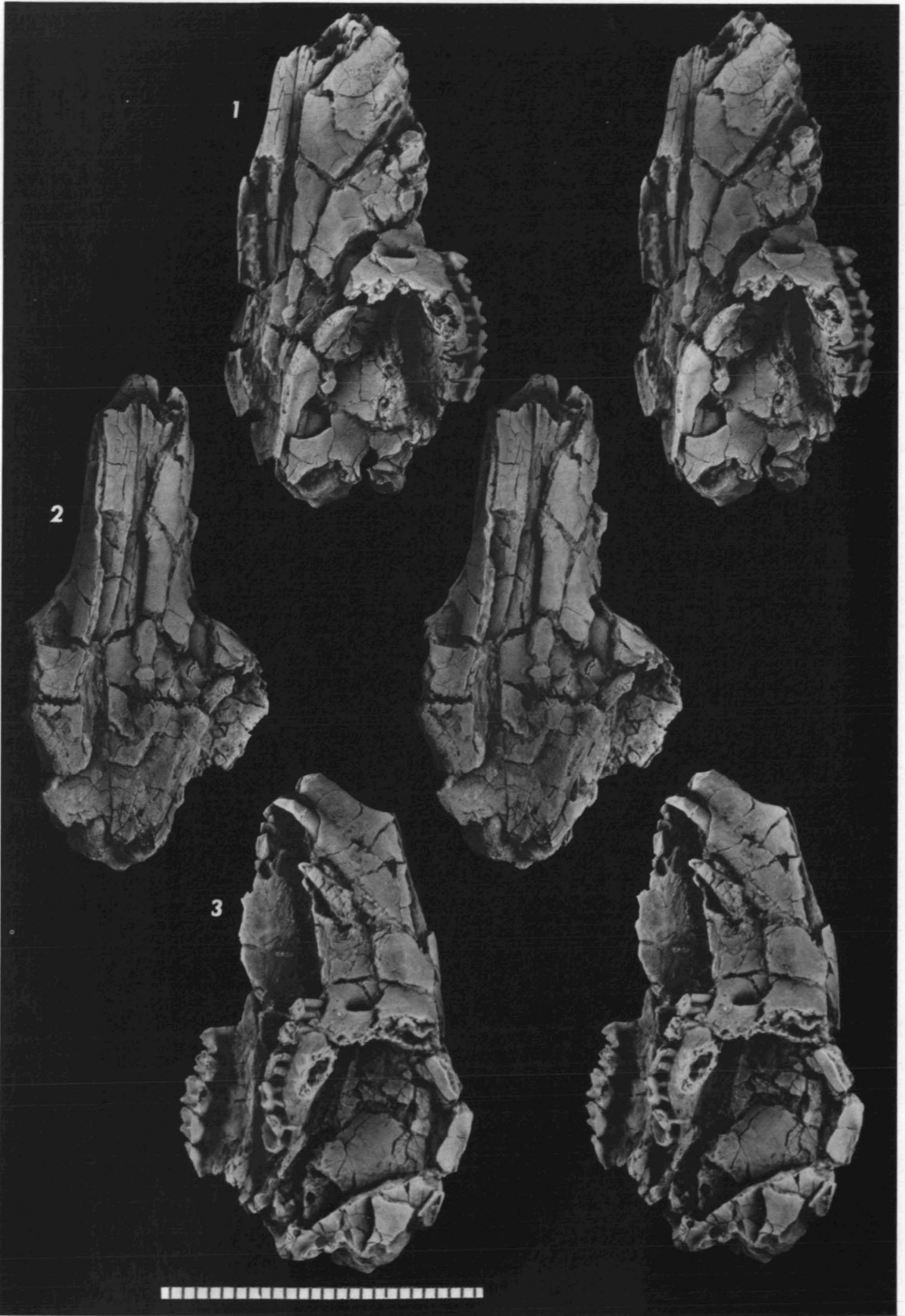
The skull contains a nearly complete upper dentition, lacking only the crowns of the enlarged medial incisors, the right lateral incisor, and the right canine. Measurements are provided in Table 1. The upper dental formula is 2.1.2.3. It differs from all other plesiadapiforms now known in the definite presence of only two upper premolars (all others have three). The medial incisor was large, with the root laterally compressed. A gap at the midline separates the roots of the left and right medial incisors, but their crowns were almost surely in contact. Immediately following the medial incisor is the much smaller lateral incisor. It is also laterally compressed and is about half the diameter of the medial incisor. The crown of I² preserved on the left side of the skull is high and caniniform (Pl. 1, fig. 3). A short diastema, which contains the premaxillary-maxillary suture, separates the lateral incisor

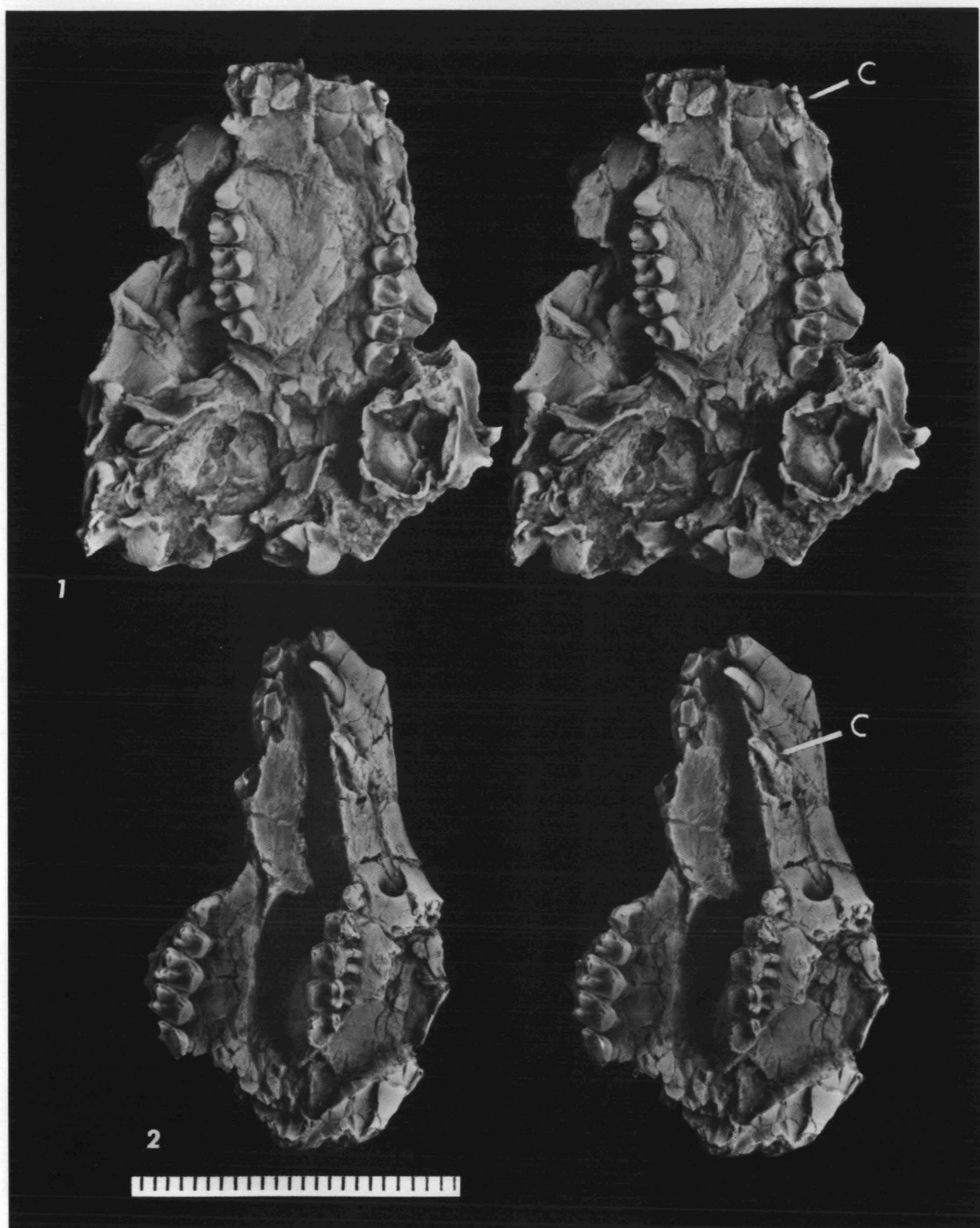
EXPLANATION OF PLATE 1

(Twice natural size; scale is in mm)

Figures 1-3 — *Ignacius graybullianus*, UM 65569.

- 1 — Lateral view showing right side of rostrum and right orbital wall.
- 2 — Dorsal aspect.
- 3 — Lateral view of left side.

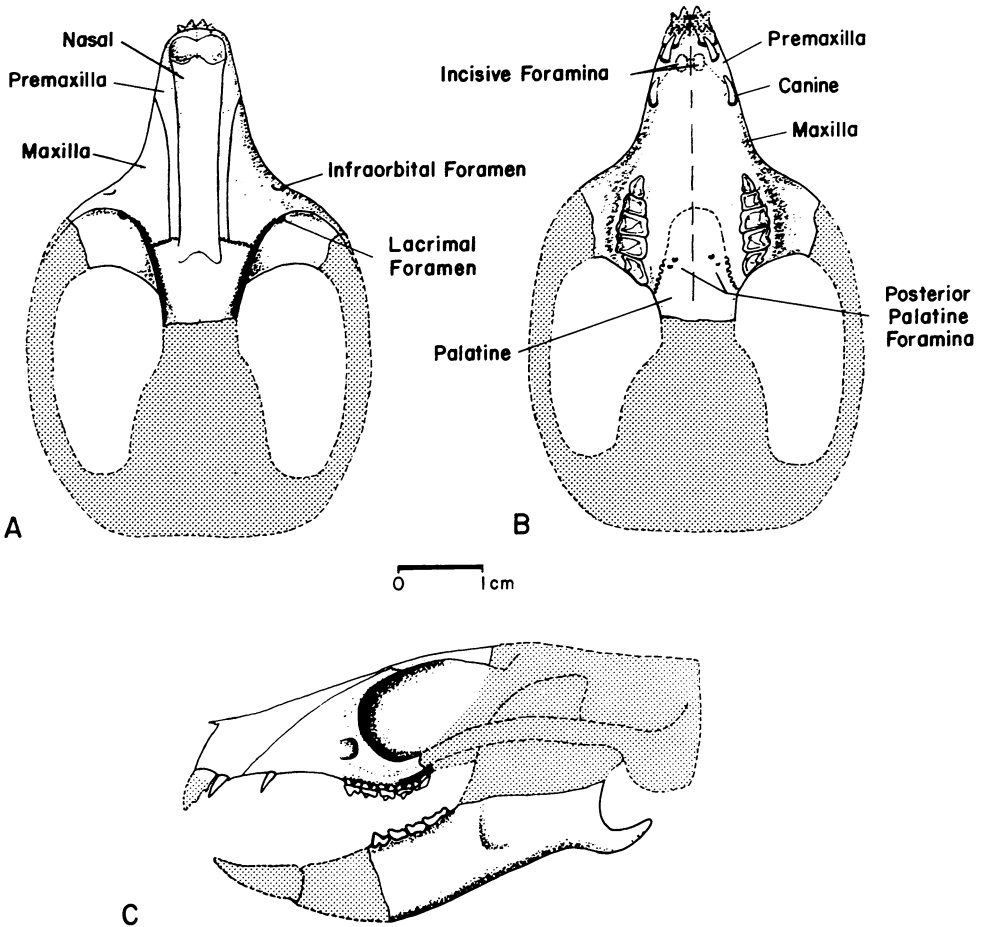




EXPLANATION OF PLATE 2

(Both figures twice natural size; scale is in mm)

Figure 1 – *Phenacolemur jepseni*, AMNH 48005, ventral aspect.Figure 2 – *Ignacius graybullianus*, UM 65569, ventral aspect. “C” indicates single-rooted caniniform canine.



TEXT-FIGURE 1 – Reconstruction of the skull of *Ignacius graybullianus*, based on UM 65569. (A) Dorsal aspect. (B) Ventral aspect. (C) Lateral aspect.

from the canine. The canine is slightly smaller than the lateral incisor and is somewhat lower crowned, but it is otherwise similar to the lateral incisor. The damaged crown of the left canine is preserved in the specimen, but it has been dislodged from its alveolus and now lies anterior to it, making it more anteriorly inclined than it was originally. The incisors and canine were all slightly procumbent.

The cheek tooth series, beginning with P^3 , is separated from the canine by a long diastema about twice the length of the one between the canine and the lateral incisor (Pl. 1, fig. 3; Pl. 2, fig. 2). The right cheek tooth series is much better preserved than the left and is the basis for the following description. P^3 is longer than wide and roughly triangular, being broad behind and tapering anteriorly. The large paracone on P^3 is preceded by an anterolingual-curving crest, and followed by a low, very small metacone. A very low, tiny cuspule lies posterolingual to the latter. P^3 has two roots, one anterior and one posterior. P^4 is larger relative to M^1 than in the holotype of *Ignacius graybullianus*, but otherwise P^4 - M^2 are like those in the previously known specimens. They have flattened crowns with very low relief and a strongly oblique centrocrista – diagnostic characteristics of *Ignacius*. Though very close in size to contemporary *Phenacolemur praecox*, they are relatively broader, with squared rather than rounded posterior margins. M^3 in the new specimen has a greatly expanded posterointernal basin, comparable to the condition in *Phenacolemur praecox* and *P. jepseni*. This contrasts with the

condition of M^3 previously considered diagnostic for *Ignacius* (see Bown and Rose, 1976), suggesting that this feature is variable.

The skull has been fractured and distorted by compression, causing some elements to overlap and obscure others. Although the extent of all of the visible bones is not completely clear, most can be delineated with reasonable assurance.

The snout tapers noticeably toward the front and is comparatively long and narrow, much more so than in *Carpolestes* (Rose, 1975) and *Palaechthon* (Wilson and Szalay, 1972; Kay and Cartmill, 1974), but not unlike that of *Plesiadapis* (Russell, 1964; Gingerich, 1976) or *Microsypops* (McKenna, 1966; Szalay, 1969). The nasals are narrow and long, projecting back beyond the level of the antorbital margin, probably slightly farther than the fronto-maxillary suture (Pl. 1, fig. 2; Text-fig. 1). They are broadest anteriorly, where they constitute almost the entire breadth of the snout, and taper somewhat posteriorly. The anterior border of each nasal is concave, with the medial margin projecting farthest forward. The nasals are generally similar to those of *Plesiadapis* but are much broader and slightly longer relative to the size of the skull. The premaxillae form much of the lateral wall of the rostrum (Pl. 1, fig. 1; Text-fig. 1); their original position seems to have been sub-vertical. They are large, much larger than they appear to have been in *Carpolestes* and *Microsypops*, but less broad than in *Plesiadapis*. They narrow posteriorly, extending back just beyond the level of the antorbital margin, and appear to contact the frontals. (Unfortunately this region is visible only on the right side, where there are several fractures; it is obscured by overlapping and hard matrix on the left side.) Premaxillary-frontal contact is associated with enlarged procumbent incisors in many mammals, for example, rodents, lagomorphs, the marsupial *Dactylopsila*, and the primate *Daubentonia* (Gingerich, 1971), as well as *Plesiadapis* (Russell, 1964).

The maxilla is moderately large, although its posterodorsal limit is unclear because the extent of the lacrimal cannot be ascertained. Opening above P^3 is a very large, single infraorbital foramen (Pl. 1, fig. 3), through which passed the maxillary nerve (V^2). This feature, comparable to the condition in *Palaechthon* and *Plesiadapis*, is found in living mammals that possess a well-developed rhinarium and facial vibrissae, and has been interpreted in *Palaechthon* to indicate well-developed tactile and olfactory senses (Kay and Cartmill, 1974). This is, of course, to be expected in archaic mammals, and very probably was true for *Ignacius* as well.

Although the boundaries of the lacrimals are not clear, the relatively large lacrimal foramen is visible within the anterior margin of the orbit (Pl. 1, fig. 3; Text-fig. 1). This contrasts with the position in *Plesiadapis* and many extant prosimians, in which the lacrimal lies just outside the orbit, but it is similar to the position in extant rodents, lagomorphs, and lipotyphlans, and in proteutherian "insectivores" such as *Kennalestes* (Kielan-Jaworowska, 1968) and *Leptictis*. Because of crushing, it is difficult to determine the interorbital breadth. However, it appears to be relatively less than in *Palaechthon* as reconstructed by Kay and Cartmill (1974). (Allowing for distortion, this dimension is roughly 17-20 mm in *Ignacius*.)

The anterior border of the frontals runs from the orbital wall medially toward and almost perpendicular to the mid-sagittal plane (Pl. 1, fig. 2; Text-fig. 1), in contrast to the almost parasagittal orientation of this border in *Plesiadapis*. Its convoluted suture is well marked until, near the midline, fracturing obscures the precise points where the nasals and premaxillae meet the frontals. The supraorbital margins are rugose, particularly on the frontals. This rugosity appears to have continued forward to the antorbital margins (now damaged), where it may have marked the insertion of facial musculature, as in *Leptictis* ("Ictops," Butler, 1956). The supraorbital crests converge posteriorly but do not meet on the preserved section of the frontals. Thus a sagittal crest, if present, was situated farther back than the preserved part of the skull.

The orbits and anteriormost part of the temporal fossa are preserved, but they are too crushed to reveal any details of the orbital wall. The angle between the orbital planes and the sagittal plane cannot be determined with any accuracy, but it does not appear to differ much from that in other plesiadapiforms.

The specimen is broken through the frontals just anterior to the postorbital constriction. At this point, a cast of the relatively large olfactory bulbs is preserved just beneath the back of the frontals

TABLE 1 – Dimensions of the upper dentition and skull of *Ignacius graybullianus*, UM 65569 (in mm).

Medial incisor,	L: 2.30*	
	B: 1.35*	
Lateral incisor,	L: 1.60*	
	B: 1.05*	
	H: 2.95*	
Canine,	L: 1.35*	
	B: 0.90 approx.*	
P ³ ,	L: 2.05	
	B: 1.50	
P ⁴ ,	L: 2.00	
	B: 2.50	
M ¹ ,	L: 2.40	
	B: 3.35	
M ² ,	L: 2.25	
	B: 3.25	
M ³ ,	L: 2.55	
	B: 2.50	
Diastema between lateral incisor and canine:		3.7 approx.
Diastema between canine and P ³ :		6.8
Breadth of anterior of rostrum across both nasals:		7.0 approx.
Length of nasals:		24.0 approx.
Palatal length from anterior of medial incisor alveolus to back of palate:		33.0 approx.

* Dimensions of incisors and canine are anteroposterior diameter at alveolar border (L) and transverse diameter at alveolar border (B). Crown height (H) of lateral incisor is measured from anterior alveolar border to tip of crown.

(Pl. 1, fig. 2). Their size and position approximates that in *Plesiadapis* (Gingerich, 1976) and would seem to be further evidence that *Ignacius* depended to a large degree on olfaction.

DISCUSSION

Whereas *Palaechthon* and *Microsypops* are cranially generalized plesiadapiform primates, *Ignacius* is among the most specialized. Its skull configuration is superficially like that of rodents and rabbits, largely due to the elongate snout and long diastema shared by all of them. This may well be adaptively significant. Plesiadapiform primates have sometimes been considered primitive ecological analogues of rodents, and *Ignacius* is the most rodentlike among them.

A reconstruction of the skull of *Ignacius* is present in Text-figure 1. Some points of comparison with other plesiadapiform crania have already been noted. In general skull shape, *Ignacius* is closer to *Plesiadapis* than to *Palaechthon* or *Carpolestes*, which may be more a consequence of their similar adaptations than an indication of particular affinity. That this configuration was arrived at in parallel is evidenced by the different proportions and suture patterns of the skull elements. The closest common ancestor of both *Ignacius* and *Plesiadapis* was no younger than early Paleocene and must have had a skull much more like that of *Palaechthon*.

Ignacius is one of three genera comprising the Paromomyidae, which also include *Paromomys* (middle Paleocene) and *Phenacolemur* (late Paleocene-middle Eocene) (see Bown and Rose, 1976). *Paromomys*, the probable ancestor of both *Ignacius* and *Phenacolemur*, is known only from jaws

and teeth. Only one skull of *Phenacolemur* that reveals any structure has been recovered (Simpson, 1955; Szalay, 1972), but this specimen, *P. jepseni* (AMNH 48005, see Pl. 2, fig. 1), is too crushed to provide any information on the front half of the skull, aside from the dentition. Nevertheless, what it reveals about the teeth is highly instructive. The palate of *P. jepseni* contains four teeth anterior to the molars, interpreted by Simpson (1955) as the canine and three premolars; this remains the most reasonable interpretation.* Although *P. jepseni* postdates *Ignacius graybullianus*, it retains an additional tooth in the upper cheek tooth series. Moreover, both P² and the canine are two rooted, thus sharply contrasting with *Ignacius*. The canine is separated from P² by a short diastema, and P² from P³ by a slightly longer gap. The distance separating P³ from the canine, though occupied by P², is shorter than the corresponding diastema in *Ignacius*.

Late Tiffanian *Phenacolemur pagei* also contrasts with *Ignacius*. In the former, P² is two rooted and slightly smaller than P³, but otherwise similar. It is situated immediately in front of P³. Anterior to P² and separated from it by a short diastema is a smaller tooth, indicated by a bilobed root, perhaps divided within the alveolus (PU 19498); presumably this is the canine, as in *P. jepseni*. Early Wasatchian *Phenacolemur praecox* is probably a direct descendant of *P. pagei* and may lie near the ancestry of *P. jepseni*. Its anterior upper teeth unfortunately are not known, but it seems reasonable to speculate that it retained both a two-rooted P² and a two-rooted canine. It is interesting to note that *P. praecox* and *I. graybullianus* have been found at the same sites in the Bighorn Basin, and their molars are almost exactly the same size. They can be easily distinguished, however, by the much lower and flatter crowned cheek teeth and the much smaller P⁴ in *Ignacius*, as well as by a number of detailed aspects of molar morphology.

In all known species of *Phenacolemur*, all teeth in the mandible between the single enlarged incisor and P₄ have been lost. This is also true for some species of *Ignacius*, but at least some individuals of late Paleocene *Ignacius* still retained P₃. The ancestral middle Paleocene *Paromomys* possessed three lower premolars, which suggests that the ultimate reduction of the mandibular dentition was achieved independently in *Ignacius* and *Phenacolemur*.

Until recently, *Ignacius* has been almost universally regarded as a synonym of *Phenacolemur*. Bown and Rose (1976) recently resurrected the name *Ignacius* on the basis of a number of features of P⁴-M³ that seem to distinguish at least two lines that evolved independently, though in parallel, since middle Paleocene time. Comparison of the anterior upper teeth in the skull herein described with those in species of *Phenacolemur* lends additional support to generic separation of *Ignacius* and contributes to the evidence that by the early Eocene these genera had been evolving independently for a considerable time.

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* Szalay (1972:61) stated that the palate holds a small, two-rooted canine followed by P² on the left side, whereas the right P² is preceded immediately by "the root of an enlarged anterior incisor." Minor cleaning reveals that the right P², like the left, is preceded by a small two-rooted tooth, the root dimensions of which compare exactly with those of the left canine. Thus no evidence of the upper incisors is preserved in this specimen.

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