# FIELDIANA

## Geology

NEW SERIES, NO. 21

# *Protoptychus hatcheri* Scott, 1895 The Mammalian Faunas of the Washakie Formation, Eocene Age, of Southern Wyoming. Part II. The Adobetown Member, Middle Division (= Washakie B), Twka/2 (In Part)

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Murra, J. 1946. The historic tribes of Ecuador, pp. 785-821. In Steward, J. H., ed., Handbook of South American Indians. Vol. 2, The Andean Civilizations. Bulletin 143, Bureau of American Ethnology, Smithsonian Institution, Washington, D.C.

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# *Protoptychus hatcheri* Scott, 1895 The Mammalian Faunas of the Washakie Formation, Eocene Age, of Southern Wyoming. Part II. The Adobetown Member, Middle Division (= Washakie B), Twka/2 (In Part)

## Abstract/Dedication

This report was originally intended for the festschrift honoring Philip Hershkovitz (Patterson & Timm, 1987). I was unable to complete it in time for inclusion in that volume and subsequent events have caused further delays. It deals with a highly specialized Eocene rodent that is of particular interest paleontologically, anatomically, and ecologically. Intriguing, partially unresolved, phylogenetic considerations concerning its relationships are discussed. These suggest broader implications for rodent systematics.

I expand upon the prior descriptions of the skull and teeth, and describe for the first time details of skeletal morphology of this jerboa-like species, *Protoptychus hatcheri* Scott, 1895, with its enlarged elongated hind limbs and greatly expanded auditory bullae, features that so aptly characterize these ricochetal creatures. The descriptions are based upon specimens recovered, mostly from a single locality, within the Washakie Basin of southwestern Wyoming.

*Protoptychus* lived in a subtropical environment during the late Middle Eocene in Wyoming and Utah. The associated faunal and floral elements included alligators; softshelled turtles; rhinoceroses; a variety of insectivores, primates, and rodents; and palm trees. All have living members that usually are limited to the tropics or subtropics. Some other faunal associates such as gar fish, uintatheres, titanotheres, tillodonts, taeniodonts, achaenodonts, and hyopsodonts were probably similarly circumscribed, but the evidence for this is more tenuous; from wherever they are known, they are associated with the same or similar suites of tropically restricted forms.

Stratigraphy, regional geology, and lithology give evidence of abundant stream channel and floodplain deposits. Doubtless, the main drainages supported some sort of riverine forests, and perhaps these extended along the borders of the intermittent ponds or central lake(s). But the presence of the jerboa-like *Protoptychus* suggests that the broad divides between the narrow, but lush, forested centripetal drainages of the Basin were probably arid, because today all such highly specialized living creatures occupy arid or semiarid environments.

Phil, with his wide appreciation of ecological and environmental relationships of the modern faunas and with his extensive works on rodents, will be as intrigued by this animal as anyone. I therefore dedicate this account to him, for he is an esteemed and helpful friend and colleague. We have shared many, often lengthy and always stimulating, discussions of dental morphology and evolution, and sometimes these strayed into far more wide-ranging topics. For all of this, I am pleased to honor him in this manner.

## Introduction

This study reports on an extinct and until now poorly known rodent genus that is remarkably specialized for hopping and turning with ricochetal movements in a manner very like that seen in modern jerboas, if we may infer the habits of the fossil form from the known locomotion and anatomy of its reasonable living analogues. In fact, in as much as the genus, *Protoptychus,* is the earliest form to attain such a specialization, all later ones must be considered as being convergent upon it, if not actually descendant from it. The two most striking specialized features correlated with this distinctive way of life are greatly lengthened hind limbs and tremendously enlarged auditory bullae. That great elongation of hind limbs should be correlated with specialized hopping is intuitively reasonable, but that such extreme bullar specializations, which are only partially understood, should be, is far less clear.

## Geology, Stratigraphy, and Localities

*Protoptychus* is known only from Middle Eocene, Uintan deposits of the Uinta and Washakie Basins (Berggren et al., 1985) from stratigraphic units that on the basis of faunal and stratigraphic correlations appear to be nearly contemporaneous. Krishtalka et al. (1987) reviewed the earlier works that paved the way for the modern stratigraphic interpretations and gave details for both the correlations and the bases upon which they stand. A modified segment of their correlation chart is given (fig. 1). It represents slightly more than the 15 MY of Eocene time, and shows where within the late Middle Eocene the *Protoptychus* fossils occur.

All but two of the recognized specimens of *Protoptychus* from the Washakie Formation are from a single locality, FM-8-57-WDT, located in W½, SE¼, Sec. 13, T15N, R98W, Sweetwater County, Wyoming (USGS Kinney Spring, Wyoming Quadrangle, 7.5 minute series). The locality is also shown on the map of the NW Quadrant of the Washakie Basin (Turnbull, 1978, pl. 2, p. 589), where it is designated as being in the S½ of that section. It is within the Adobetown Member, in its middle division, Twka/2, of Roehler (1973) and Turnbull (1978). This middle portion of the member corresponds to the Upper Washakie (= Washakie B) of Granger (1909) and others. The bed itself is near to the level of Roehler's Bed 640, although there is some uncertainty about the precise correlations of the beds and levels in this portion of the section.

The precise locality is one of several subdivisions of the above-designated general locality called the *Protoptychus* locality; it is shown in Figure 2. It lies near the base of the *Protoptychus* sandstone unit, which is more than 30 ft (9 m) thick, lightly indurated, and crossbedded throughout. Capping the unit is a more heavily indurated subdivision about 6 in. (15 cm) thick that forms the lip of the rim in the area and protrudes to the east out from under the dune cover at the track. All of the beds in this area have an E–SE dip (about E 120 degrees) of variable inclination near to but not exceeding 7.5 degrees.

The *Protoptychus* locality itself, which includes several natural alcoves on each side of the one that produced the two partial skeletons, has produced several hundred identifiable fragments of various small mammals as well as some reptile and bird remains. The associated mammals include marsupials, insectivores, primates, carnivores, condylarths, perissodactyls, and rodents (both *Protoptychus* and several other taxa). Most of the fossils consist of scattered and broken pieces that either had weathered out, or were removed, from thin lenticular stringers of pebbles, small bones, or bone chips and teeth that lay along certain of the bedding planes of the otherwise nearly barren sandstone unit. The two nearly complete, articulated specimens of *Protoptychus* that constitute the heart of this discussion (figs. 3, 4) are exceptions in that they were not a part of any of the bonebearing lenses, but lay several centimeters below one of the more extensive of these stringers. The two animals may have died in their burrows, although we found no traces of burrow infillings to support this idea, or they may by chance have been buried and preserved before scavengers got to them. Most of the missing parts were lost to weathering during exposure, but some of the skeletal elements may have been scavenged shortly post mortem (left manus of PM 8018, part of the rear quarters of PM 39371).

## Materials
## Order Rodentia
## Suborder Protrogomorpha
## Family Protoptychidae

***Protoptychus*** **Scott, 1895**

***P. hatcheri*** Scott, 1895 (including *P. smithi* Wilson, 1937).

The prime specimens identified as *P. hatcheri* from locality FM-8-57-WDT are PM 8018 (fig. 3)

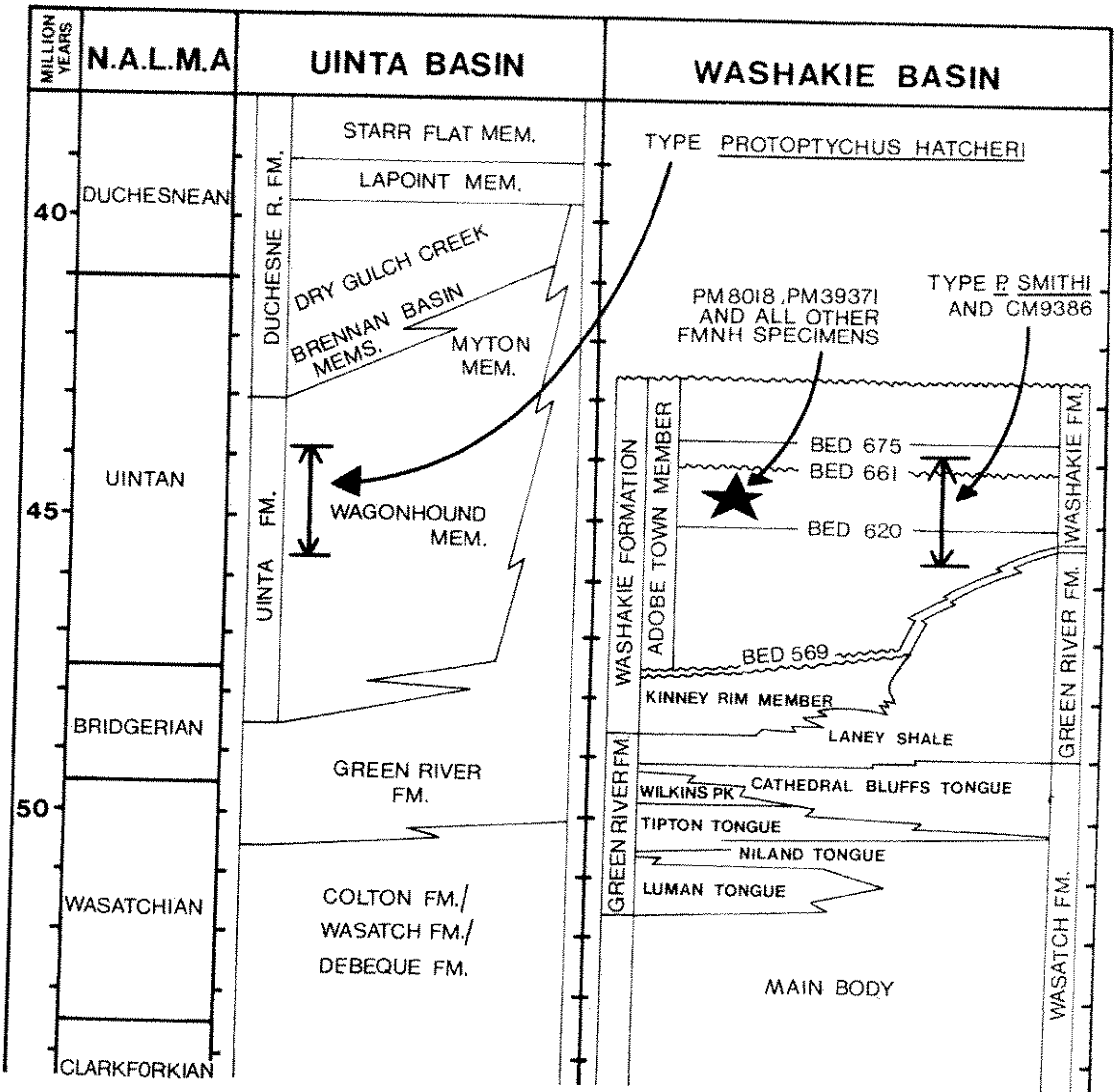

FIG. 1. Correlation chart for the Eocene sediments of the Uinta and Washakie Basins, with approximate levels of all of the known *Protoptychus* specimens indicated. The type of *P. hatcheri* is from Kennedy's hole, Upper Uinta B. Most of the others (star) are from one locality at the base of the *Protoptychus* SS unit, Bed 640, of the middle division (Twka/2) of the Adobetown Member, i.e., within the Washakie B of other workers.

and PM 39371 (fig. 4). Both are nearly complete skeletons. The first was discovered in 1959 (field number W-7-59) lying on its right side as shown in the figure. The then exposed portions (the few bleached white areas of bone) suggested that possibly there were two animals present, to judge by the disproportionate sizes of the exposed limb bones. Preparation proved otherwise, and the large rear quarters proved to be connected to the small and delicate ribs, front limbs, and skull. Unknown to us at the time, there was another skeleton within three feet of the first and in a similar position, also on its right side, but more nearly on its back then the other; it lay unexposed and undetected. It became exposed through weathering a decade later and was collected (field number T-69-3).

Repeated collecting at this locality has produced 69 specimens referred to this taxon; mostly these are maxillary or mandibular remains. All are listed in the Appendix. The sample is large enough to provide an assessment of dental detail, variation, and wear.

FIG. 2. Three views of the part of the Field Museum's *Protoptychus* locality (FM-8-57-WDT) that yielded most of the specimens. The fossils were found eroding out of the base of the exposed part of the *Protoptychus* sandstone where the man is seen prospecting. In all there are five natural alcoves eroded into the bluff; the three richest ones are numbered on the photo in A. The other less productive alcoves lie to the left and right of those shown. **A,** Overview, looking south over the intervening wash at the three main alcoves, seen from the top of an erosional remnant ridge that protrudes to the east into the erosional badlands from the edge of the Adobetown Rim (see Turnbull, 1978, pp. 589–590, 594). **B,** View looking southeast while standing on the productive level of the *Protoptychus* sandstone within alcove #3, part of which is seen in the foreground and to the lower right. Alcove #2 (with figure) is in the middleground, and alcove #1 is hidden behind and to the left of the sandstone ridge immediately behind the prospector. **C,** View looking northeast from the deepest point of alcove #2. Both of the Field Museum skeletons came from the area just toward the viewer, to the left of where I am prospecting. Note the landmark feature on the horizon, an erosional remnant pillar about 45 ft above the microfaunal level.

Of the two other specimens of *Protoptychus* known, or believed, to have come from the Washakie, the best is a Carnegie Museum specimen (CM 9386, fig. 5) which came from near the Northwest flank of Haystack Mountain (i.e., western end of the Mammoth Buttes of Cope, 1884) from an area located about a mile east of Manuel Gap, along the Manuel Road across Adobetown. This would place it somewhere near the section line between sections 26 and 27 of T16N, R97W, (Manuel Gap Quadrangle, Sweetwater County, Wyoming) about halfway between my localities FM-2-56-WDT and FM-3-56-WDT, nearest FM-1-56-WDT. This is shown on the same NW Quadrant map as the main *Protoptychus* locality (Turnbull, 1978, pl. 2), and lies four miles NNE of it. Accordingly, this locality must be close to the Bed 640 level too, although it could be from a unit as low in the section as Bed 630, or as high as Bed 644. The specimen was found by Anne Zangerl in 1941, and she, Rainer Zangerl, and John Clark collected it, giving it Carnegie Museum field num-

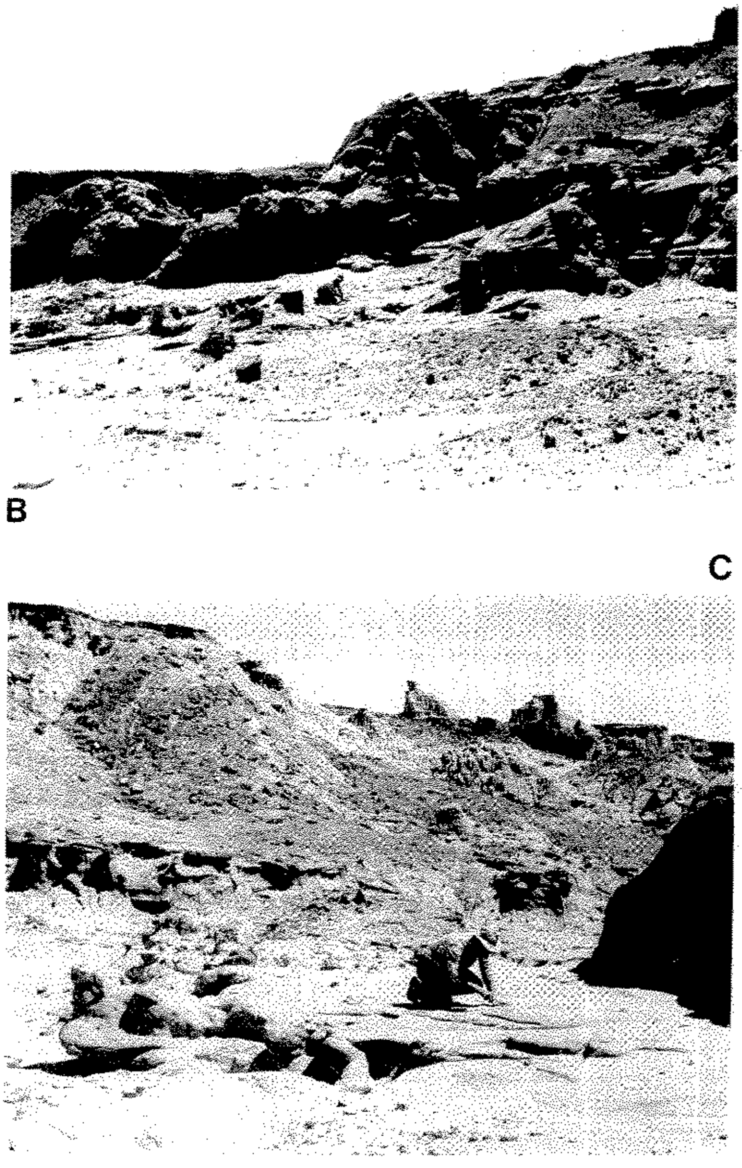

FIG. 2. Continued.

ber 2-15/1941. As found, the specimen was articulated, lying in a lightly indurated fine sandstone matrix very much like the *Protoptychus* SS, the unit that yielded the Field Museum specimens. It consisted of a partial skull and most of the skeleton. Subsequent preparation has freed many of the bones, including the skull, unfortunately at the expense of certain limb and body proportion data. Figure 5 shows the specimen in its present state, consisting of the partial skull (lacking the braincase and lower jaws), the articulated distal portion of the right hind limb (tibia, fibula, astragalus, calcaneum, and another tarsal), part of the left hind limb (proximal half femur and metatarsals II, III, and IV), four presacral vertebrae (three lumbar and one posterior thoracic or anteriormost lumbar), most of the sacrum, and an articulated string of six of the proximal caudal vertebrae, two distal

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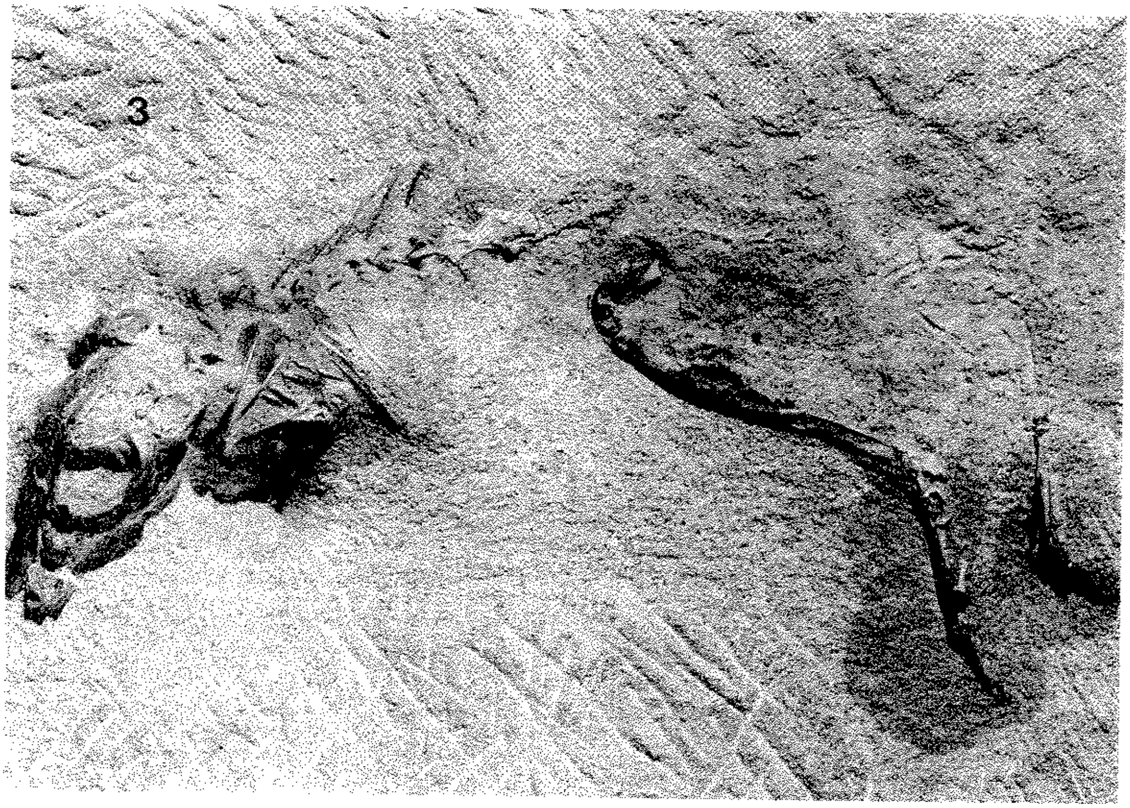

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caudals, the right ulna, and some loose and/or broken foot bones and scraps.

The other specimen purported to be from the Washakie is the type of *Protoptychus*? *smithi* Wilson, 1937, Yale Peabody Museum specimen number 13189. It consists of a fragment of a left maxillary with $P^4$–$M^2$ and is here referred to as *P. hatcheri.* Locality data for this specimen are poor and quite vague (35 mi. south of Black Buttes). Wilson (1937, pp. 447, 451–452) has reviewed the situation and discussed the problem at some length, and arrived at the conclusion that

> . . . it is most probable that PROTOPTYCHUS? SMITHI is from beds of upper Bridger or lower Uinta age in the Washakie Basin. Geographic evidence points to the former age. Stage of evolution of the fragmentary rodent fauna indicates an upper Eocene assemblage. The author favors an Uinta age for the Yale species.

We now know that there are Uintan aged beds on the Northwest flank of Haystack Mt. and the Adobetown Rim areas adjacent it, and that these outcrop areas lie even closer to Black Butte, albeit to the east–southeast not south, than does Haystack Mt. proper, which is even farther east and was the only upper Eocene stratum in the area known to Wilson in 1937. Hence, the geographic problem is lessened, and Wilson's conclusion is reinforced by the presence of Uintan outcrops closer to Black Butte. Furthermore, for the early workers the area of the northwest flank of Haystack would have been most easily worked from either Red Dog Buttes (now known to be most likely the old Tadpole stage station north of Haystack Mt. proper, *fide* P. Robinson, pers. comm.) or from the LaClede station. Both abandoned stagecoach stations on the old overland trail served as base camps for some of the early Yale collecting parties, and both were accessible from the Union Pacific railroad via Bitter Creek station. I show *P. smithi* here for comparison in Figure 6A.

Unfortunately, until now the type species of the genus *Protoptychus, P. hatcheri,* has been known only from its holotype, PU 11235, the well-preserved skull of an aged animal, and according to Wahlert (1973) from another specimen that I have not seen, "a much damaged facial region, PU 11230." (Albert Wood in his criticism of this manuscript says, "When I last saw 11230, it was an edentulous skull.") In the type, the dentition had reached a fairly advanced stage of wear and much detail of the original crown features of its teeth had been worn away in life. It was found in the Uinta Basin, Wagonhound Member of the Uinta Formation, and thus it and the Washakie specimens are of approximately the same age (fig. 1). It is illustrated in Figure 6B.

## Descriptions

(See Table 1 for measurements.)

### Skull and Bulla

Wahlert (1973) has made the most recent scholarly study of the type specimen. He updated and refined the description of the skull beyond that given by Scott (1895), and he revised the various earlier interpretations regarding its systematic position such as those of Winge (1941) and Klingener (1964). For the cranium Wahlert noted a series of features, many of which had been noted by Scott, but he then commented on those deemed to be of significance in determining relationships of the genus (Wahlert, 1973, pp. 6–8), and devoted the remainder of the study to an interpretative discussion of the possible and probable relationships. I have little to add to Wahlert's description and discussion, and rather than repeat it, I simply follow his format in the same order for the Field Museum specimens, adding comments where appropriate:

1) POSTERIOR EXTENSIONS OF THE NASALS—Because of the uniqueness of this feature among rodents, it is useful for characterizing the genus, but gives little insight into relationships.

2) AUDITORY REGION—Here I have several comments and some descriptive additions. The bullae are indeed greatly inflated. They are so expanded dorsally and ventrally that they come close

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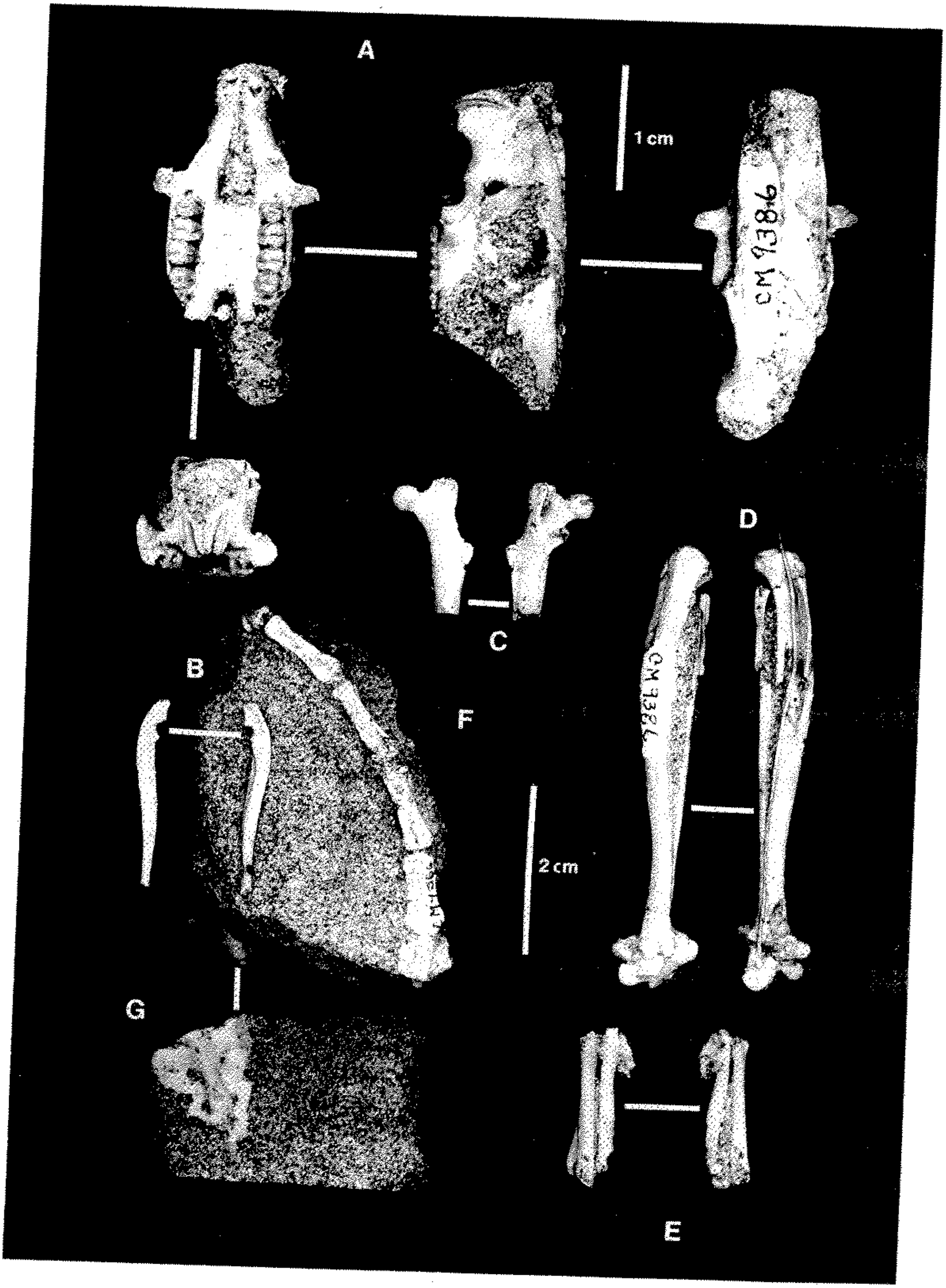
FIG. 3. The first Field Museum *Protoptychus* skeleton, PM 8018. Note that the left bulla is damaged and the left manus, pelvis, and tail, as well as portions of both hind limbs, are missing. The huge right bulla can be seen to protrude and surround the parietal–occipital region and to reach up to the midline of the skull. The disproportionate size relationships between fore and hind limbs is evident even without the complete femur. Approximately ×1.

FIG. 4. The second Field Museum *Protoptychus* skeleton, PM 39371. Approximately ×1.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to meeting at the midline both above and below the cranium. But the inflation, which involves temporal, mastoid, and occipital portions of the skull, is actually the result of inflation of tympanic, mastoid, and (?) exoccipital bones with the mastoid expanded into the temporal region. Damage from exposure prior to its discovery has resulted in the left bulla of PM 8018 being opened dorsolaterally and dorsoposteriorly to reveal something of the internal structure. Within the damaged bulla, one can discern that the major portion of the (dorsal) mastoid chamber was broadly open in its ventral portion, for the damage has opened it nearly to its base, a dividing septum that remains intact anteromedially. The opening extends well into the posterior, (?) occipital/mastoid chamber to reveal a small bit of its floor posteriorly. This floor is also a presumed septal partition separating the occipital chamber from the main ventral tympanic chamber. The damaged area extends down to the meatal opening which either is totally obliterated, or if not is a broad hollow trough that immediately rolls ventrally into the main tympanic chamber near its lateral wall. Medial to this, near the medial wall of the bulla, there is a convexly rounded structure that I take to be part of the petrosal (promontorium), but no clearly identifiable features are exposed.

3) Parietal–Bullar Relationships—Here I find some degree of variation. Wahlert had noted that in the type the parietal overlapped the dorsal (mastoid) epitympanic sinus portion of the bulla, and I find this to be the case in PM 39371 also. However, in the right bulla of PM 8018, in which the bulla is more expanded dorsally (and perhaps also slightly distorted in that direction), it is the bulla that overlaps the parietal and even the interparietal.

4) Cranial Foramina—The incisive foramina are indeed elongate. I interpret this as a specialization of unknown significance. It is quite comparable to the condition in *Jaculus j. flavillus* in which the posterior margins have migrated back to the same level with respect to $M^1$ ($P^4$ missing or vestigial in *Jaculus*), and the premaxillary–maxillary suture intersects the lateral margin of the foramen in a similar anterior position.

5) Infraorbital Foramen—The infraorbital foramen is, as Wahlert (1973) stated, "considerably larger dorsoventrally than that of any protrogomorphous rodent." I measure it to be 0.66 cm in the type (0.49 to the dorsal step within the long axis of the oval opening) by ~0.23 cm maximum in the shorter, lateral axis of the oval. For the Field Museum and Carnegie Museum specimens the comparable measures are: PM 8018, left = 0.65 cm × ~0.20 cm; PM 39371, left and right = 0.60 cm × ~0.21 cm; CM 9386, long axes of both left and right are estimated to be about 6 mm, but no short axis measure is possible.

Wahlert thus concluded (1973, p. 7), "*Protoptychus* was hystricomorphous." In the sense that the foramen is greatly enlarged over all protrogomorphous forms, it does suggest the hystrico-

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Fig. 5. The Carnegie Museum specimen of *Protoptychus*, CM 9386, as it is today. **A,** Ventral, left lateral, dorsal, and front views of the skull. **B,** Approximately lateral and medial views of right ulna. **C,** Anterior and posterior views of proximal half, left femur. **D,** Posterolateral and anteromedial views of left tibia, fibula, astragalus, calcaneum, and one other tarsal in articulation as found. **E,** Nearly dorsal and ventral views of the left metatarsus. **F,** Articulated string of four complete and two partial proximal caudal vertebrae, about numbers 11 through 17 to judge by the reduction of processes and relative lengths. **G,** Dorsal (mostly hidden) and ventral views of the sacrum.

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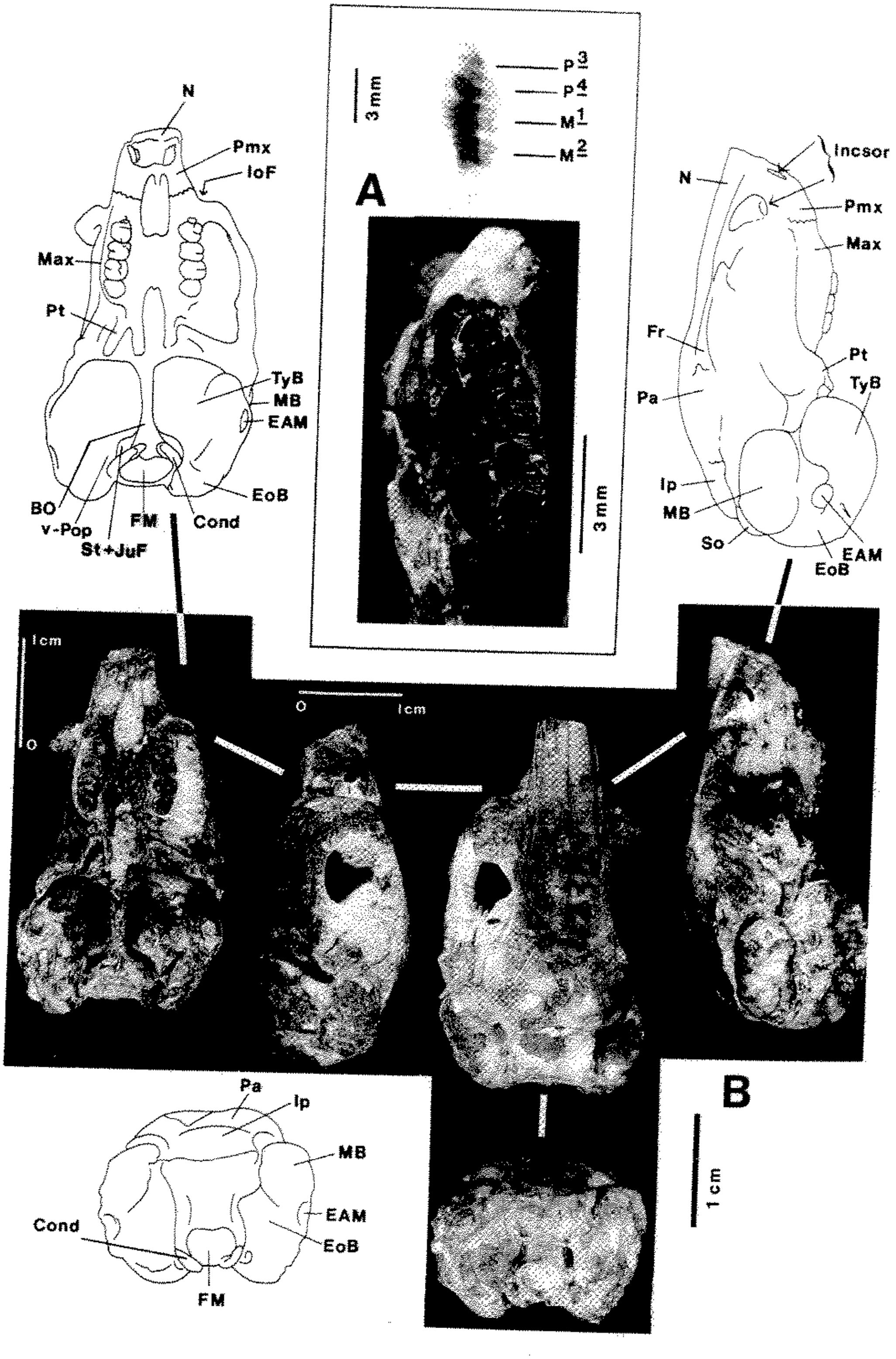
Fig. 6. **A,** The Yale University specimen, the type of *Protoptychus smithi* Wilson, YPM 13189, a left maxillary shown in ventral view. Note the faint trace of the filled alveolus of the $P^3$. It can also be seen (in side view) in the x-ray (above). **B,** The Princeton University specimen, the type of *Protoptychus hatcheri* Scott, PU 11235, shown in ventral, left lateral, dorsal, right lateral, and posterior views. Outline drawings are labeled according to the following scheme: BO = basioccipital bone, Cond = condyle, EAM = external auditory meatus, EoB = exoccipital portion of bulla, FM = foramen magnum, Fr = frontal bone, Incisor = upper incisor on broken section and in "window" near the infraorbital foramen, IoF = infraorbital foramen, Ip = interparietal bone, $M^1$ and $M^2$ = upper molars 1 and 2, Max = maxillary bone, MB = mastoid portion of bulla, N = nasal bone, $P^3$ and $P^4$ = upper premolars 3 and 4, Pa = parietal bone, Pmx = premaxillary bone, Pt = pterygoid bone, So = supraoccipital bone, St + JuF = location of stapedial and jugular foramina, TyB = true tympanic portion of bulla, v-Pop = vestigial paroccipital process. **C,** *Protoptychus hatcheri*, PM 8018. Skull and jaws shown in left lateral and left anteroventral views, and skull in posterior view. **D,** *Protoptychus hatcheri*, PM 39371. Skull and jaws in left lateral view and in ventral view with the left jaw ramus removed to expose the left upper dentition.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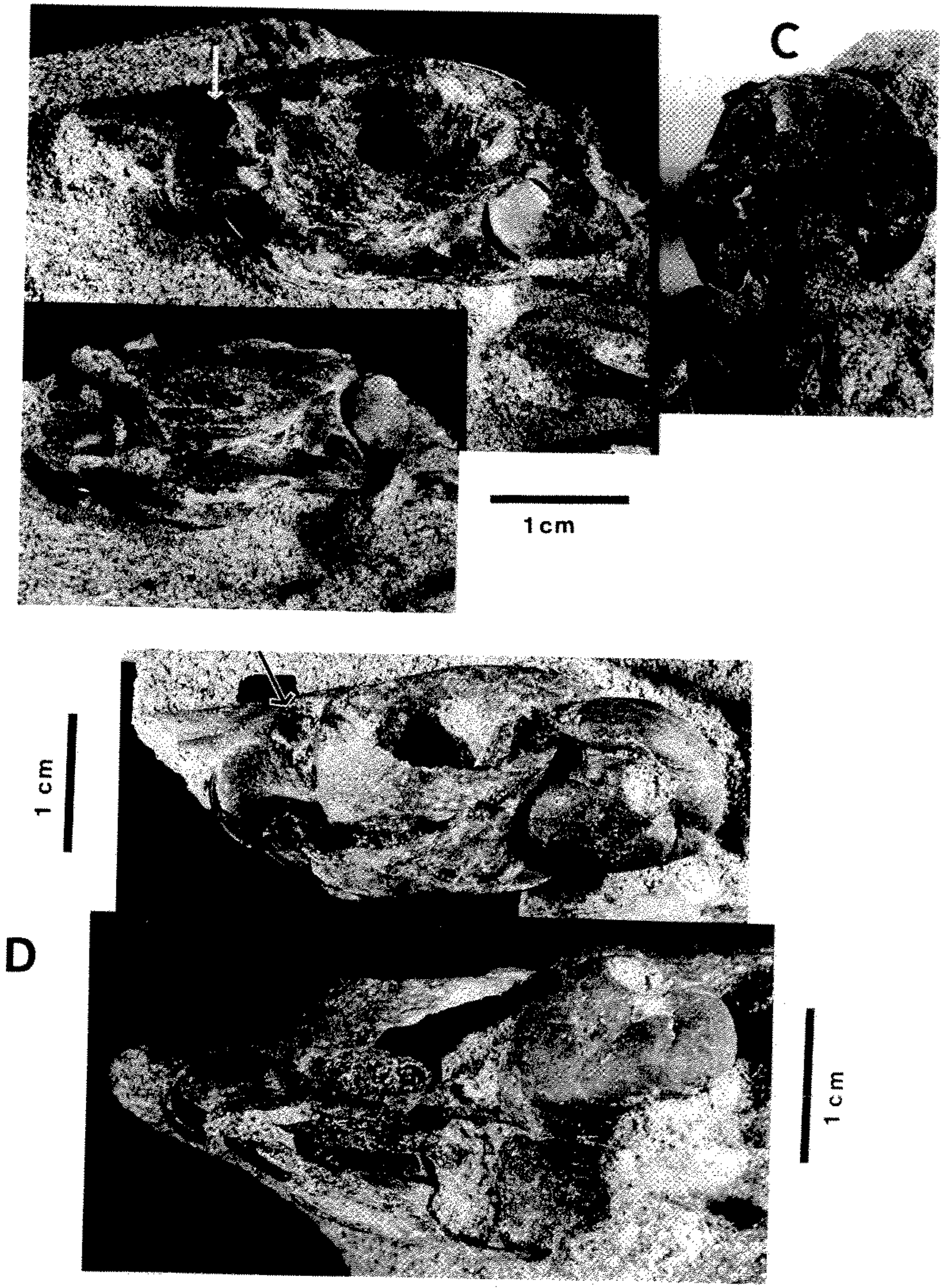
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TABLE 1. Measurements (in mm) of some features of the skull and jaws of various specimens of *Protoptychus*.

| | ***hatcheri*** **Type** | ***smithi*** **Type** | ***hatcheri*** | | | | | |
|---|---|---|---|---|---|---|---|---|
| | **PU 11235** | **YPM 13189** | **CM 9386** | **PM 8018** | **PM 39371** | **PM 2084** | **PM 2303** | **PM 2304** |
| Skull | | | | | | | | |
| Length | >32 | — | — | 33.8 | ~33 | — | — | — |
| Greatest breadth (zygoma) | ≥19 | — | ≫14.2 | * | ~20 | — | — | — |
| Greatest breadth (bullae) | ≤20.5 | — | — | ~21 | ~23.5 | — | — | — |
| Palate | | | | | | | | |
| Length (midline suture) | 6.2 | — | 7.4 | * | * | — | — | — |
| Width at $P^4$–$M^1$ | 4.6 | — | 4.6 | * | * | — | — | — |
| Width at $M^2$–$M^3$ | 5.2 | — | 4.8 | * | * | — | — | — |
| Bulla | | | | | | | | |
| Height | 13.9 | — | — | * | 13.3 | — | — | — |
| Anterior–posterior diameter | 13.5 | — | — | 15.4 | 14.1 | — | — | — |
| Cheektooth row | | | | | | | | |
| Length $P^4$–$M^3$ | 7.1 | — | 7.7 | * | * | — | — | 7.6+ |
| Length $P^4$–$M^2$ | 5.3 | 5.6 | 5.6 | * | * | — | — | 5.8− |
| Length $P^4$–$M^1$ | 3.5 | 3.4+ | 3.6 | * | * | ~3.6 | — | 3.8− |
| Length $M^1$–$M^2$ | 3.6 | 3.9 | 4.0 | * | * | — | — | 3.9+ |
| Length $M^1$–$M^3$ | 5.4 | — | 6.0 | * | * | — | — | 5.8+ |
| Length $M^2$–$M^3$ | | | | * | * | — | 3.8 | 3.7 |
| | **PM 8018** | **PM 39371** | **PM 2301** | **PM 2305** | **PM 2312** | **PM 2319** | **PM 2323** | **PM 2324** |
| Jaws | | | | | | | | |
| Ramus length (incisor alveolus to rear of condyle) | ~18 | ~19 | — | — | — | — | — | — |
| Ramus depth beneath $M_1$ | ~6.3 | ~6 | — | — | — | 5.2+ | — | 5.3+ |
| Height of ascending ramus (perpendicular to and above cheektooth row) | ~2.5 | ~3 | — | — | — | — | — | — |
| Cheektooth row | | | | | | | | |
| Length $P_4$–$M_3$ | * | * | — | — | — | 8.7 | — | 8.2+ |
| Length $P_4$–$M_2$ | * | * | — | — | — | 6.7 | — | 6.5+ |
| Length $P_4$–$M_1$ | * | * | 4.4 | 4.7− | 4.1− | ~4.3 | 3.8+ | 4.4+ |
| Length $M_1$–$M_3$ | * | * | — | — | — | 6.5 | — | 6.5 |
| Length $M_1$–$M_2$ | * | * | — | — | — | 4.3− | — | 4.1 |
| Length $M_2$–$M_3$ | * | * | — | — | — | 4.3+ | — | 4.5 |

* Feature present but inadequately exposed for measuring.

morphous condition. But to me it also suggests the myomorphous condition, and in fact it fits that state closer than it does the hystricomorphous state in terms of the size and proportions of the opening.

Whether hystricomorphous or myomorphous, it is the anterior portion of the zygomaticomandibularis that invades the surface of the snout via the foramen, thereby becoming the maxillomandibularis (deep masseter or masseter medialis of many authors). I have shown the condition for both a myomorph and a hystricomorph (Turnbull, 1970); I now suggest that, in as much as the myomorphous state is intermediate between the (primitive) protrogomorphous and the (most specialized) hystricomorphous states with regard to degree of invasion of the infraorbital foramen by muscle, we might do well to modify Wood's (1974) concepts slightly. I suggest that rather than consider the myomorphic condition to be "a combination of the hystricomorphous and sciuromorphous types" (Wood, 1974, p. 23) we consider it to be a structural intermediate between protrogomorphous and hystricomorphous types, with little bearing on the sciuromorphous type, which constitutes a different sort of specialization that does not involve the infraorbital foramen. Here Klingener's 1964 study of dipodoid myology is particularly informative, and although my inter-

Table 1. Continued.

| *hatcheri* | | | | | | | | Range | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **PM 2306** | **PM 2322** | **PM 8004** | **PM 8029** | **PM 37373** | **PM 37382** | **PM 37384** | **PM 37385** | **Min.** | **Max.** | **N (N)** |
| — | — | — | — | — | — | — | — | >32 | 33.80 | 3 |
| — | — | — | — | — | — | — | — | >19 | ~20 | 2 (3) |
| — | — | — | — | — | — | — | — | <20.5 | ~23.5 | 3 |
| — | — | — | — | — | — | — | — | 6.2 | 7.4 | 2 (4) |
| — | — | — | — | — | — | — | — | 4.6 | 4.6 | 2 (4) |
| — | — | — | — | — | — | — | — | 4.8 | 5.2 | 2 (4) |
| — | — | — | — | — | — | — | — | 13.3 | 13.9 | 2 (3) |
| — | — | — | — | — | — | — | — | 13.5 | 15.4 | 3 |
| — | — | 6.8+ | 7.3+ | — | 7.3 | — | 7.9− | 6.8+ | 7.9− | 7 (9) |
| ~6.1 | 5.9 | ~5.4 | ~5.4 | — | 5.7− | 5.6 | 5.9+ | ~5.4 | ~6.1 | 11 (13) |
| ~4.1 | ~3.6 | 3.4+ | 3.8+ | — | 3.8 | 3.6− | 3.9− | 3.4+ | ~4.1 | 12 (14) |
| 4.0 | 4.1 | 3.8 | ~3.9 | — | 4.0 | 3.9+ | 4.2 | 3.6 | 4.2 | 11 (13) |
| — | — | ~5.4 | 5.6+ | — | 5.9 | — | 6.2− | 5.4 | 6.2− | 7 (9) |
| — | — | 3.4+ | ~3.5 | 3.6 | 3.9− | — | — | 3.4+ | 3.9− | 9 (11) |
| **PM 8005** | **PM 8006** | **PM 8009** | **PM 8010** | **PM 8011** | **PM 39830** | **PM 39831** | **PM 39832** | | | |
| — | — | — | — | — | — | — | — | 1.8 | 1.9 | 2 |
| — | — | — | — | — | — | — | — | 5.2+ | ~6.3 | 4 |
| — | — | — | — | — | — | — | — | ~2.5 | ~3.0 | 2 |
| — | 7.8+ | 7.5+ | — | — | — | — | — | 7.5+ | 8.7 | 4 (6) |
| — | 5.7+ | 5.1+ | 6.1 | — | 6.4 | — | 5.9 | 5.1+ | 6.7 | 7 (9) |
| — | 3.7+ | 3.5− | 3.7+ | 4.1 | 4.3 | 3.7 | 3.5+ | 3.5− | 4.7+ | 13 (15) |
| — | 6.3+ | 5.7+ | — | — | — | — | — | 5.7+ | 6.5 | 4 (6) |
| — | 3.9+ | 3.6 | 4.2+ | — | 4.4− | — | ~4.2 | 3.6 | 4.3− | 7 (9) |
| 3.9 | 4.3+ | 4.1 | — | — | — | — | — | 3.9 | 4.5 | 5 (7) |

(N), potential sample size if buried structures are ever exposed.

pretation differs somewhat from his, I believe his work supports my position (see discussion on p. 14).

I find that I differ from Wahlert in a minor way in my observations concerning the snout. The sides of the snout are indeed flattened, but the course of the root of the incisor does not make much of a swelling in the type. In it and in both FMNH skeletons the only such swelling is located forward near the alveolar margin. The Carnegie specimen, however, does show the sort of swelling that Wahlert describes for the type, so that his description does fit one specimen of the species precisely. More posteriorly, the root lies deeper within the bone and enters the pit within the area just in front of the foramen, and for a short distance it appears within a "window" that opens to the surface (fig. 6D). In fact most of the medial wall of the foramen and the area in front of it, where the origin of the maxillomandibularis muscle is presumed to have been located, is multiply fenestrated. Best seen in PM 39371, this unusual muscle origin surface causes me to suspect that the muscle must have drawn off mainly from the unfenestrate peripheral parts of the area, or perhaps from a superficial aponeurosis that also was anchored peripherally.

6) Foramina of Orbital Region and 7) Sphenoidal Fissure, etc.—For these two cat-

egories of Wahlert's, I have no additions or further comments. For these foramina in particular and for many of the others as well, Wahlert (1974) is a most helpful reference.

8) Postglenoid, Temporal, etc. Foramina—I believe that the apparent absence of the postglenoid foramen may be as much the result of reduction of the glenoid as it is due to bullar inflation. As for the apparent absence of the temporal foramen, bullar inflation doubtless is the cause; it may not actually be absent, but just masked by the inflation and the pathway from it hidden. The exit could be almost anywhere along the slit between the dorsal bullar chamber and the parietal bone. With regard to a carotid canal, I cannot pinpoint it on either of the better preserved FMNH specimens, but the jugular foramen and the fissure medial the bulla could well provide access, so I see no compelling reason to assume its absence. The stapedial foramen (seen only in the type) opens laterally within the common pit for it and the jugular foramen, just lateral to the occipital condyles. It is located in the identical position as is that foramen in modern *Jaculus.*

At this point it is worth while to look beyond *Protoptychus* at conditions in its living analogues. Klingener (1964) reported the masseter muscle of dipodoids to be hystricomorphous. He gave two criteria: 1) "M. masseter lateralis profundus does not extend anterodorsad on a zygomatic plate, as it does in myomorphous and sciuromorphous types," and 2) "Part of M. masseter medialis anterior originates from the rostrum anterior to the infraorbital foramen and passes posteroventrad through the foramen to insert on the mandible, in contrast to the sciuromorphous and protrogomorphous types."

These two criteria are important and figure frequently in the remainder of this discussion, and in Figure 12. For ease in discussing them, I simply use "Zygomatic Plate" to carry the full meaning of Klingener's first criterion, and "I.O.F." for his second. Most rodent specialists now agree that the protrogomorphous type is primitive and generalized, and that the other three types represent specialized advances, all providing enhanced incisor function through greater leverage advantage of the masseter. From here on, there is less uniformity of opinion. I believe that each of the three specializations is distinctive. That of the sciuromorphous type, involving as it does the superficial masseter and a Zygomatic Plate, goes off in one direction while that of the hystricomorphous type, involving the deep masseter and the I.O.F., goes in a distinctly different direction. Those roden that 'discovered and used' both ways of enhanci masseter function, we have come to know as m omorphous types. This specialization, while ma ing use of both of the others, is in a sense inte mediate, but I contend is just as distinctive. T degree of use of the I.O.F. is always limited—nev reaching the maximum extent seen in advance hystricomorphous types, and the extent of Zyg matic Plate development varies between little an the full-blown degree of most myomorphous form

Klingener (1964) concluded that the myomo phous masseter of muroids could have evolve from any of the other three types. He believed th while all are possible ancestral types, only the hy tricomorphous type is the most likely. To me, de ivation from the protrogomorphous type appea to be most likely. For it to be derived from eith of the other two specialized types would invol some degree of reversal of one or both sorts specialization of the masseter. Hence, I see th myomorphous type as a distinct specialization its own right, one in which both superficial an deep masseter adjustments were involved togeth er. Thus from the protrogomorphous type all thre specialized types evolved independently: sciur morphous by Zygomatic Plate development, hy tricomorphous by I.O.F. invasion, and myomo phous by both. This seems most parsimonious that each specialized route is independent, and n reversing of a specialized trend is required.

## **Mandibles** (Figure 7)

(See Table 1 for jaw measurements.)

The jaws of *Protoptychus* are delicately buil more massive in the areas surrounding the denta region than elsewhere, and the horizontal ramu is relatively deep. The ascending ramus is thin narrow, and elongated. The condyle is small an oval in its occlusal outline with its long axis aligne with the anteroposteriorly elongated glenoid. Th coronoid process is a spikelike extension of th anterior edge of the ascending ramus. This re markably elongate coronoid appears to be a mod ification in response to raised posterior area o muscle origin resulting from the extreme bulla inflation. The angular process draws off from th lateral side of the jaw, lateral to the incisor, behin the last molar. This is best seen in PM 2319, whic is broken across the region near the forming "root" end of the hypsodont incisor. Thus *Protoptychu*

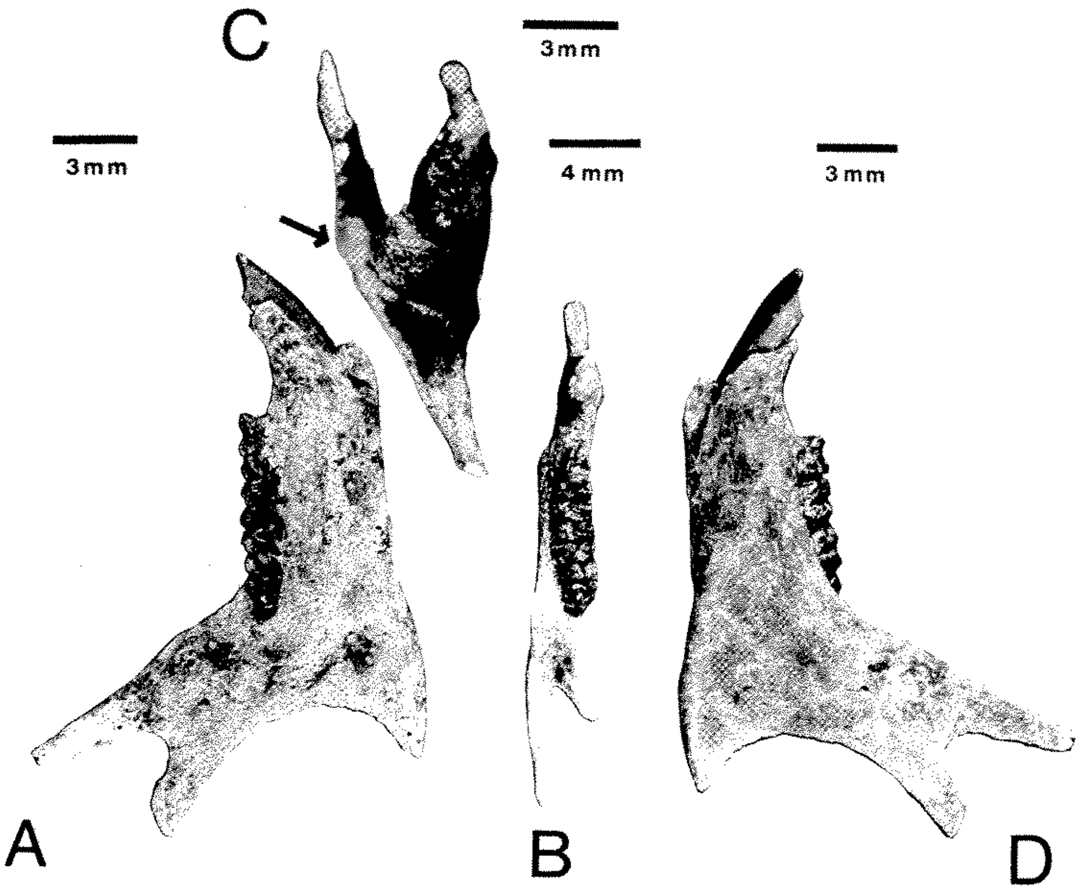


FIG. 7. *Protoptychus hatcheri*, PM 39371, left lower jaw. **A,** lingual view. **B,** dorsal view. **C,** posterior view. **D,** lateral view. In **C,** the arrow points to the condyle of the jaw.

is weakly or incipiently hystricognathous, but I do not find this feature to be a very satisfactory character because all sciurognathous–hystricognathous distinctions are blurred for the primitive hystricognathous condition. I therefore consider this feature to be at most a weak indication of the direction of evolution rather than accepting it as indicative of the full-blown shift from the sciurognathous state. The symphysis is short, relatively small, and far forward beneath the anterior half of the diastema. The mental foramen is located beneath the posterior half of the diastema. It is usually oval, but may have a slight constriction in its middle (PM 39371). The masseteric fossa is shallow but extensive and distinct. There is a noticeable boss just dorsal to its anterior, pointed end, lateral to the $P_4$. I now believe that I misled Wahlert in 1973 with my statement about a pars reflexa of the masseter muscle. The ventral edge of the ramus does look as though there might have been one, but it could not have been very large and I can see no demarcation of an insertion field where it would be expected along the groove beneath the root of the incisor or low on the medial side of the jaw.

## Dentition

(See Table 1 for toothrow dimensions and Tables 2–4 for individual tooth measurements.)

The dental formula is $I^1_1$, $C^0_0$, $P^2_1$, $M^3_3$. This is contrary to that originally stated for the species (and for *P. smithi*). Both Wilson (1937) and Wahlert (1973) reported the presence of the minute $P^3$ of *P. hatcheri,* and Wahlert shows it in his figure 1. Scott had missed the little peglike $P^3$, which is so reduced a tooth that it probably had no function beyond serving as a buttress for the $P^4$. In the type

Table 2. *Protoptychus* upper cheektooth measurements (in mm).

| | $P^3$ | | $P^4$ | | |
|---|---|---|---|---|---|
| | L | W | L | AW | PW |
| *P. hatcheri* type | | | | | |
| PU 11235 | 0.5− | 0.5+ | 1.6 | 1.7 | 1.8+ |
| *P. smithi* type | (alv.) | (alv.) | | | |
| YPM 13189 | ~0.4 | ~0.4 | 1.6 | ~1.7 | ~1.8 |
| *P. hatcheri* | (alv) | (alv) | | | |
| CM 9386 | 0.5+ | 0.5+ | 1.6+ | 1.7− | 2.0+ |
| PM 8018 | ~0.5 | ~0.5 | 1.9+ | * | * |
| PM 39371 | 0.6+ | 0.5− | 1.8 | 1.8 | 1.8 |
| PM 2084 | — | — | 1.4+ | 1.7 | 1.9− |
| PM 2302 | 0.8 (alv.) | 0.7 | — | — | — |
| PM 2303 | — | — | — | — | — |
| PM 2304 | 0.6+ (alv.) | 0.6 | 1.6− | 2.0− | 2.1 |
| PM 2306 | 0.5+ (alv.) | 0.5+ | 1.9+<br>(alv.) | 2.0− | 1.8 |
| PM 2307 | | | | | |
| PM 2321 | ~0.6 (alv.) | 0.5 | 1.6− | 1.8+ | 2.0− |
| PM 2322 | 0.5+ (alv.) | 0.5+ | 1.7− | ~2.0 | ~1.8 |
| PM | | | | | |
| PM 8004 | 0.5+ (root) | 0.3+ | 1.2+ | 1.9− | ~1.9 |
| PM 8007 | ~0.7 (alv.) | 0.7+ | ~1.5 | ~2.1<br>(alv.) | ~2.0 |
| PM 8008 (all alv.) | 0.7+ | 0.5+ | 1.4+ | ~2.0 | ~2.0 |
| PM 8029 | 0.7+ (alv.) | 0.7+ | ~1.8 | ~2.2 | 2.3 |
| PM 37373 | — | — | — | — | — |
| PM 37381 | ~0.8 (alv.) | ~0.7 | ~1.8 | ~2.1 | ~2.4 |
| PM 37382 | 0.4+ | 0.4+ | 1.6+ | 2.1− | 2.0 |
| PM 37384 | 0.8− | 0.7 | 1.5+ | 2.0+ | 2.0 |
| PM 37385 | ~0.9 (alv.) | ~0.9 | 1.6 | 2.2− | 2.3 |
| PM 39824 | 0.5 (root) | 0.4 | — | 2.0 | (root) |
| Obs. range | | | | | |
| Min. | 0.4 | 0.3 | 1.2 | 1.7 | 1.8 |
| Max. | 0.9 | 0.9 | 1.9 | 2.2 | 2.4 |
| N | 18 | 18 | 17 | 17 | 16 |
| Mean | 0.54 | 0.56 | 1.61 | 1.95 | 2.01 |

L, length; W, width; AW, anterior width; PW, posterior width; b, broken.

specimen it is present on the left side, missing on the right, but its root and alveolus are apparent (fig. 6B). It is indeed surprising that such a careful worker as Scott missed seeing it. In *P. smithi* no tooth is present in the $P^3$ position, but there is, I believe, a trace of one, which Wilson might have seen had he had the evidence of an x-ray photo of the specimen. Only an indistinct vestige of a small alveolus gives evidence of its presence, to judge by the appearance of the bone surface just anterior to the $P^4$. It was a small, single-rooted tooth that appears to have been shed in life (fig. 6A). Its alveolus was remodeled, partly filled, and nearly obliterated, as the x-ray confirms (fig. 6A). In my larger sample, in every case in which the appropriate area is preserved, the tooth (or its root or alveolus) is present, but it does vary considerably in size from a diameter of about 0.4 mm to 0. mm (table 2). In as much as these measures wer taken on whatever structure was available (tootl root, or alveolus), the variation is doubtless exaggerated. The larger sample thus demonstrat the consistent presence of a $P^3$ in the species, a well as its variable size and crown structure.

I find Wahlert's description of the upper dentition to be satisfactory in every detail. The suit of specimens now at hand shows the spectrum c wear stages for most teeth (fig. 8A–G); most notable in this regard is the unerupted $P^4$ of specime PM 39371 (fig. 8G), which is in its pristine condition. The best preserved $P^3$ has a crown divide into anterior and posterior moieties, the posterio being taller, and it has a worn tip. The upper dentition is shown in a conventional diagram (fig. 8H

TABLE 2. Continued.

| $M^1$ | | | $M^2$ | | | $M^3$ | | |
|---|---|---|---|---|---|---|---|---|
| L | AW | PW | L | AW | PW | L | AW | PW |
| 1.8− | 2.1 | 2.0 | 1.8− | 1.9+ | 1.8− | 1.8 | 1.8+ | 1.5+ |
| 2.0− | 2.3 | 2.0 | 1.8− | 2.0+ | 1.8+ | — | — | — |
| 2.0 | 2.1 | 2.2 | 2.0− | 2.2+ | 2.1+ | 1.7+ | 2.0− | 1.7− |
| * | * | * | * | * | * | * | * | * |
| 1.9+ | 2.1+ | 2.2− | 1.9− | 2.0+ | 2.0+ | 1.7− | 1.9+ | 1.7+ |
| ~1.8 | 2.0 | b | — | — | — | — | — | — |
| — | — | — | — | — | — | — | — | — |
| 1.7+ | 1.9+ | 1.9 | 1.8 | 1.9+ | 1.9 | — | — | — |
| 2.1− | 2.3+ | 2.3 | 2.0− | 2.1 | 2.0 | 1.7+ | 1.9 | 1.5+ |
| ~2.0 | 2.3 | 2.2 | ~1.9 | 2.1− | 1.9+ | — | — | — |
| — | — | — | — | — | — | — | — | — |
| ~1.8 | ~2.5 | 2.5 | 2.1 | 2.2+ | 2.1+ | — | — | — |
| 1.9− | 2.0+ | ~2.1 | 1.9 | 2.2+ | 2.2− | — | — | — |
| ~1.6 | ~2.2<br>(alv.) | ~2.2+ | — | ~2.3<br>(alv.) | — | — | — | — |
| ~1.9 | ~2.7 | ~2.3 | ~1.8 | ~2.2 | ~2.1 | — | ~1.6 | — |
| 1.8+ | ~2.4 | 2.2 | 1.8+ | 2.2− | 2.0+ | ~1.5 | 2.0+ | ~1.7 |
| (root) | 2.0+ | 2.0+ | 1.8 | 2.2+ | 2.1− | 1.6+ | 1.8 | 1.7+ |
| — | ~2.7 | — | — | — | — | — | — | — |
| 2.0− | 2.2− | 2.2− | 2.0− | 2.1+ | 2.0 | 1.8+ | 1.8 | 1.7− |
| 1.9+ | 2.2− | 2.3 | 2.0− | 2.2− | 2.2− | — | — | — |
| 2.1− | 2.5 | 2.6 | 2.0 | 2.4− | 2.2 | 1.9+ | 2.2− | 2.0+ |
| — | — | — | — | — | — | — | — | — |
| 1.6 | 1.9 | 1.9 | 1.8 | 1.9 | 1.8 | 1.5 | 1.6 | 1.5 |
| 2.1 | 2.7 | 2.6 | 2.1 | 2.4 | 2.2 | 1.9 | 2.2 | 2.0 |
| 16 | 16 | 16 | 14 | 15 | 14 | 7 | 8 | 7 |
| 1.89 | 2.24 | 2.20 | 1.91 | 2.15 | 2.03 | 1.71 | 1.89 | 1.69 |

* Feature present but insufficiently exposed for measurement.

of crown features, labeled to follow closely the scheme used by Wood (1962, p. 8). Bivariate plots (length by width or anterior width) for each of the upper teeth show all of the measurable specimens (collected prior to the 1986 field season) including the types of *P. hatcheri* and *P. smithi* (fig. 10).

For the lower dentition a similar suite of wear stages is now available (figs. 8J, 9), and a diagram comparable to that for the upper dentition is presented (fig. 8I). The lower incisor is enamel-covered on its slightly wider, gently curved ventral surface. This form, and the oval cross section, cause the chisel-shaped worn anterior end to be beveled. The $P_4$ is elongate with a complete but small trigonid. Its talonid is larger than the trigonid and the talonid basin has a small cuspule in its center. The hypolophid is bent with a posterior kink in its ridge between hypoconid and entoconid. The ridged hypoconulid connects with both hypoconid and entoconid, and there is a valley between it and the entoconid. The lower molars are lophate, but the lophs are interrupted in the early wear stages. The protolophid, connecting protoconid and metaconid, lies far forward at the anterior edge of the crown. The hypolophid is distinct and straight in both $M_1$ and $M_2$, but $M_3$ lacks this feature in its reduced posterior region. The short, broad, and deep talonid basin enters from the labial side and divides each tooth into anterior and posterior moieties.

As was done with the upper teeth, bivariate plots of the lower teeth have been made (fig. 10), and they all appear to be reasonably tight, as might be expected for samples from a single taxon. Because

TABLE 3. *Protoptychus hatcheri* lower cheektooth measurements (in mm).

| | $dP_4$ | | | $P_4$ | | |
|---|---|---|---|---|---|---|
| | **L** | **AW** | **PW** | **L** | **AW** | **PW** |
| PM 8018 | — | — | — | * | * | * |
| PM 39371 | 1.7+ | 1.1 | 1.4 | — | — | — |
| PM 2100 | — | — | — | — | — | — |
| PM 2301 | 1.8+ | 1.1 | 1.2 | — | — | — |
| PM 2312 | — | — | — | 1.7+ | 1.1+ | 1.6− |
| PM 2319 | — | — | — | 2.1− | 1.4− | 1.8 |
| | | | alv. | | | |
| PM 2323 | — | — | — | ~1.6 | 1.4− | 1.5 |
| PM 2324 | — | — | — | ~1.8 | ~1.3 | ~1.6 |
| PM 2326 | — | — | — | 1.8 | 1.3 | ~1.5 |
| PM 8005 | — | — | — | — | — | — |
| PM 8006 | — | — | — | w1.3 | — | b>1.0 |
| PM 8009 | — | — | — | 1.5 | 1.3 | 1.4− |
| PM 8010 | ~1.8 | w>1.0 | w1.3− | — | — | — |
| PM 8011 | — | — | — | 1.7 | 1.5 | 1.6 |
| PM 37375 | — | — | — | — | — | — |
| PM 37376 | — | — | — | — | — | — |
| PM 39829 | — | — | — | — | — | — |
| PM 39830 | — | — | — | 1.9− | 1.5+ | 1.6+ |
| PM 39831 | — | — | — | w1.9+ | w1.0+ | w1.3+ |
| PM 39832 | — | — | — | b~1.8 | b~1.2 | 1.4+ |
| Obs. range | | | | | | |
| Min. | 1.7 | 1.0 | 1.2 | 1.3 | 1.0 | 1.0 |
| Max. | 1.8 | 1.1 | 1.4 | 1.9 | 1.5 | 1.8 |
| N | 3 | 3 | 3 | 10 | 10 | 9 |
| Mean | 1.77 | 1.07 | 1.30 | 1.70 | 1.30 | 1.50 |
| ±SE | — | — | — | 0.19 | 0.16 | 0.11 |

L, length; AW, anterior width; PW, posterior width; b, broken; r, root; w, worn.

all sample sizes are small, no statistical assessments were attempted.

## Postcranial Skeleton

Table 5 presents a series of measurements of *Protoptychus* and some modern ricochetal rodents, Table 6 gives a schematic view of the vertebral column as preserved in the three partial skeletons, and Figure 11 compares limb and body proportions of *Protoptychus* and some comparative specimens. For comparative purposes three published studies provide a sound basis: Lyon (1901), Hatt (1932), and Howell (1932).

VERTEBRAL COLUMN AND RIBS—Description of the details of the vertebral column, in spite of the existence of three partial skeletons, must remain incomplete. For the two articulated skeletons, much remains buried in matrix, and I dare not risk further preparation of either for fear of causing unacceptable damage. I have been unable to get sufficient x-ray penetration of the imbedding matrix to provide a clear picture adequate to give vert bral counts, let alone details of form. Nor has computerized CAT scan resolved these details. F the other "skeleton," the Carnegie specimen, mai of the vertebrae which had been present originall or represented by impressions, are now missin probably destroyed by the preparation efforts mac shortly after its discovery. The sandstone matr is not the most ideal medium for preservation ( such delicate remains. Once removed from the matrix they readily disintegrate, even when give great care. Unfortunately, use of penetrating harc eners, which is essential in dealing with such de icate materials, was not attempted in this case. I Table 6 the status of each vertebra and rib for eac of the three specimens is shown. The cervicals ar largely buried in matrix in both PM 8018 and P 39371. In the former, enough shows to reveal tha the dorsal side of the neural arch of the atlas consists of a slender, arching, spineless strut of bone Of the axis, only a bit of its apparently well-developed dorsal spine can be seen. I cannot tel whether any cervical fusions exist. The bone is no

TABLE 3. Continued.

| M₁ | | | M₂ | | | M₃ | | |
|---|---|---|---|---|---|---|---|---|
| L | AW | PW | L | AW | PW | L | AW | PW |
| * | * | * | * | * | * | * | * | * |
| 1.9 | 1.8+ | 1.9− | 1.9+ | 2.0− | 2.0− | 2.0+ | 1.8− | 1.7− |
| 1.9 | 2.0 | 1.9− | — | — | — | — | — | — |
| 2.0 | 1.8− | 1.8− | — | — | — | — | — | — |
| 2.0 | 2.0+ | 2.1+ | — | — | — | — | — | — |
| 2.1 | 1.7+ | 1.9 | 2.1 | 1.9 | 1.9 | 2.2 | 1.8 | 1.7− |
| 2.0 | 1.6 | 1.7− | — | — | — | — | — | — |
| 2.1 | 1.9− | 1.8 | 2.1 | 2.0+ | 2.1 | 2.1+ | 1.8 | 1.6+ |
| — | — | — | — | — | — | — | — | — |
| r~2.0 | r1.6− | r1.6+ | 1.9+ | 1.8+ | 1.8+ | 1.9− | 1.7− | 1.3+ |
| 1.9+ | 1.6 | 1.7 | 1.9 | 1.7− | 1.7− | r2.0− | b>1.4 | 1.5+ |
| 1.8− | 1.7 | 1.7 | 1.8− | 1.6 | 1.7 | 1.8+ | 1.4+ | 1.4− |
| 2.0 | 1.6 | 1.7 | 1.9+ | 1.7− | 1.7+ | — | — | — |
| 2.0+ | 1.8− | 1.9 | — | — | — | — | — | — |
| 1.8+ | 1.6+ | 1.7 | 1.9+ | 1.6+ | 1.7+ | — | — | — |
| — | — | — | 2.2− | 1.9 | 2.0+ | — | — | — |
| — | — | 1.7− | 1.9+ | 1.8− | 2.0− | — | 1.7− | — |
| 2.1 | 1.9− | 1.9− | 2.2− | 2.0+ | 2.2− | — | — | — |
| w1.9− | w1.4+ | w1.7+ | — | — | — | — | — | — |
| 2.0 | 1.9 | 2.0 | 2.2+ | 1.8+ | 2.0− | — | — | — |
| 1.8 | 1.4 | 1.6 | 1.8 | 1.6 | 1.7 | 1.8 | 1.4 | 1.3 |
| 2.1 | 2.0 | 2.1 | 2.2 | 2.0 | 2.2 | 2.2 | 1.8 | 1.7 |
| 15 | 15 | 15 | 12 | 12 | 12 | 5 | 7 | 6 |
| 1.97 | 1.75 | 1.83 | 1.91 | 1.82 | 1.90 | 2.00 | 1.70 | 1.53 |
| 0.10 | 0.17 | 0.13 | 0.32 | 0.15 | 0.18 | — | — | — |

* Structure present but insufficiently exposed for measurement.

mineralized enough to show on the scan, which suggests to me that fusions are unlikely.

The anterior thoracics are similarly buried in both specimens. There appear to be at least ten rib-bearing vertebrae, but as yet I cannot present any details of their structure or even be absolutely certain of their number. In PM 8018, portions of the last four rib-bearers, T-7 through T-10, are exposed dorsally behind which there are three more reduced neural spines that I take to be those of T-11 through T-13.

The lumbars apparently number seven. In PM 8018, just above the flexed knee one can see the trace of the impression of the centrum of the missing fifth lumbar. Anterior to this there is another impression with traces of bone that represent the fourth lumbar, and in series in front of it are most of lumbars #3, #2, and #1. In PM 39371 the posterior five lumbars are exposed, but the anterior two are buried. In the Carnegie specimen there are three certain lumbar vertebrae that I take to be #4, #6, and #7, and there is another vertebra that is probably lumbar #2 or #1. All of the lumbar vertebrae have expanded anterior transverse processes, least so in the anterior three, and progressively more prominent and forward-sweeping in the more posterior ones, best seen in CM 9386.

The three (or possibly four) sacrals are best seen in CM 9386 (fig. 5G). They are subequal in length, but the first has the widest and longest transverse processes for articulation with the pelvis. The second and third have progressively narrower transverse processes. All are fused into a perforate, arrow-shaped overall form with paired neurovascular perforations just lateral to the points of junction of adjacent centra. It is likely that with advanced age the fusion was increased, and the degree of articulation with the pelvis expanded posteriorly comparable to the condition seen in other mammals, including modern kangaroo rats and jerboas, but there is no direct evidence in support of this. Dorsally, there is a low neural arch and spine on each vertebra. The centra measure 0.44, 0.42, and 0.54 cm in length.

The caudals, absent on PM 8018, and nearly so on PM 39371, are best known from CM 9386,

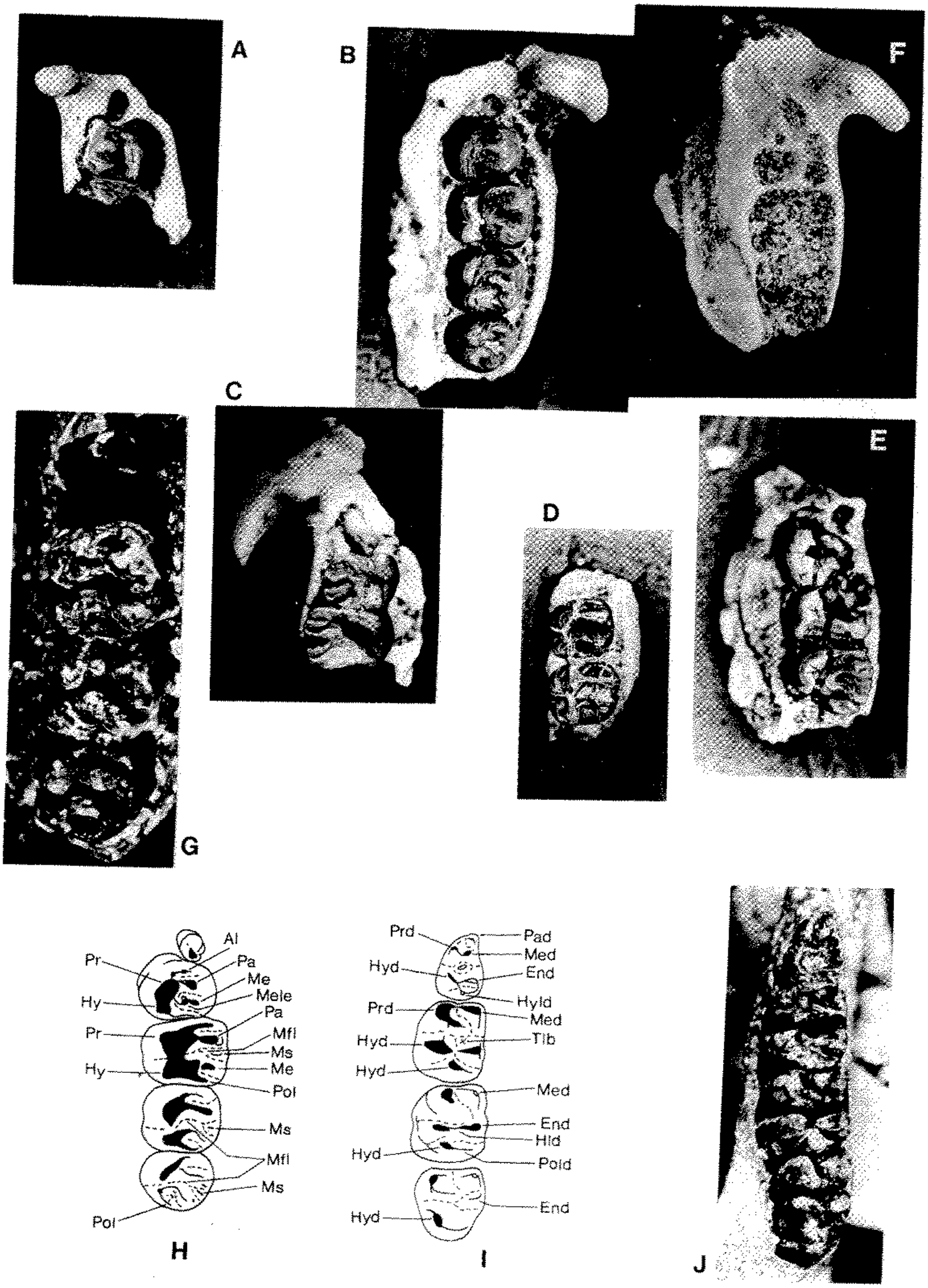
TABLE 4. Cross-section measurements of incisors of *Protoptychus hatcheri.*

| Specimen | Upper incisors | | Lower incisors | |
|---|---|---|---|---|
| | **Length (long axis)** | **Width (short axis)** | **Length (long axis)** | **Width (short a** |
| PU 11235 Type | 2.0− | 1.1− | — | — |
| CM 9386 | 2.2− | 1.5− | — | — |
| PM 8018 | 2.2+ | 1.2+ | 2.0 | 1.3 |
| PM 39371 | 2.2− | 1.1+ | 1.8 | 1.2− |
| PM 2308 | 2.3 | 1.4− | — | — |
| PM 2309 | 2.4− | 1.4− | — | — |
| PM 2310 | 2.4− | 1.4− | — | — |
| PM 2319 | — | — | 2.0− | 1.2+ |
| PM 8003 | 2.3− | 1.1+ | — | — |
| PM 8009 | — | — | (1.5) | (1.0) |
| PM 8010 | — | — | 2.0+ | 1.2 |
| PM 8011 | — | — | 1.9 | 1.2+ |
| PM 8015A | — | — | 2.0 | 1.2 |
| PM 8015B | 2.4 | 1.4 | — | — |
| PM 37377 | 1.9 | 1.1 | — | — |
| PM 39827 | 2.5+ | 1.5 | — | — |
| PM 39828? | 2.0− | 0.9+ | — | — |
| PM 39832 | — | — | 1.9− | 1.2+ |
| PM 39836 | 2.3+ | 1.4+ | — | — |
| PM 39839 | 2.6 | 1.4+ | — | — |
| N | 14 | 14 | 7 | 7 |
| Obs. range | 1.9–2.6 | 0.9–1.5 | 1.8–2.0 | 1.2–1.3 |
| $\bar{x}$ ± SE | 2.26 ± .20 | 1.28 ± .19 | 1.94 ± .08 | 1.21 ± .04 |
| Including dubious specimen | | | | |
| N | — | — | 8 | 8 |
| Obs. range | — | — | 1.5–2.0 | 1.0–1.3 |
| $\bar{x}$ ± SE | — | — | 1.89 ± .17 | 1.19 ± .08 |

which preserves parts of the midproximal five vertebrae, complete and in articulation with one another and with the proximal fragment of a sixth (fig. 5F). The first of these is short, and may be a sacral. It measures 0.81 cm, almost twice the length of each of the three usual centra of the sacrum, and possesses narrow but well-developed transverse processes. The second is elongate, measures 0.98 cm, and has traces of transverse processes anteriorly. The third, fourth, and fifth are each slightly longer than the second, measuring 1.10, 1.10, and 1.08 cm. Clearly these elongated midproximal caudals indicate that the tail was an elongated, powerful balancing organ. They are proportionately as large as, if not larger than, those of living kangaroo rats or jerboas (see table 5), all of which exceed those of nonricochetal forms.

PECTORAL GIRDLE AND FRONT LIMB—The s ula is delicate, long and narrow throughout, widest at its rounded vertebral margin (best in PM 8018, fig. 3). The spine is high and ext nearly to the margin. Supra- and infraspinatu sae are deep and elongate, the latter bordere a marginal axillary spine. Humerus, radius, ulna are correspondingly delicate. The hun head, neck, and greater and lesser tuberositie all bunched together. The shaft of the humer slender, its distal articulation broad, and the epicondylar foramen is relatively large with tr lea, capitulum, and coronoid fossa well develo as is the deltoid crest, which reaches nearl midshaft. The shaft of the radius is straight the usual tuberosity and neck beneath the cup head. Distally the articulation is unremarkabl

FIG. 8. **A–G,** A series of maxillary specimens of *Protoptychus hatcheri* demonstrate some of the variation in the population from the main locality. Specimens shown are: **A,** PM 8004. **B,** PM 2304. **C,** PM 2307. **D,** 2303. **E,** PM 2322. **F,** PM 8008. **G,** PM 39371. **H, I,** Upper and lower cheek tooth diagrams, respectively. **J,** lower cheek dentition of PM 39371. A–F are shown approximately ×6; G and J, approximately ×7.5.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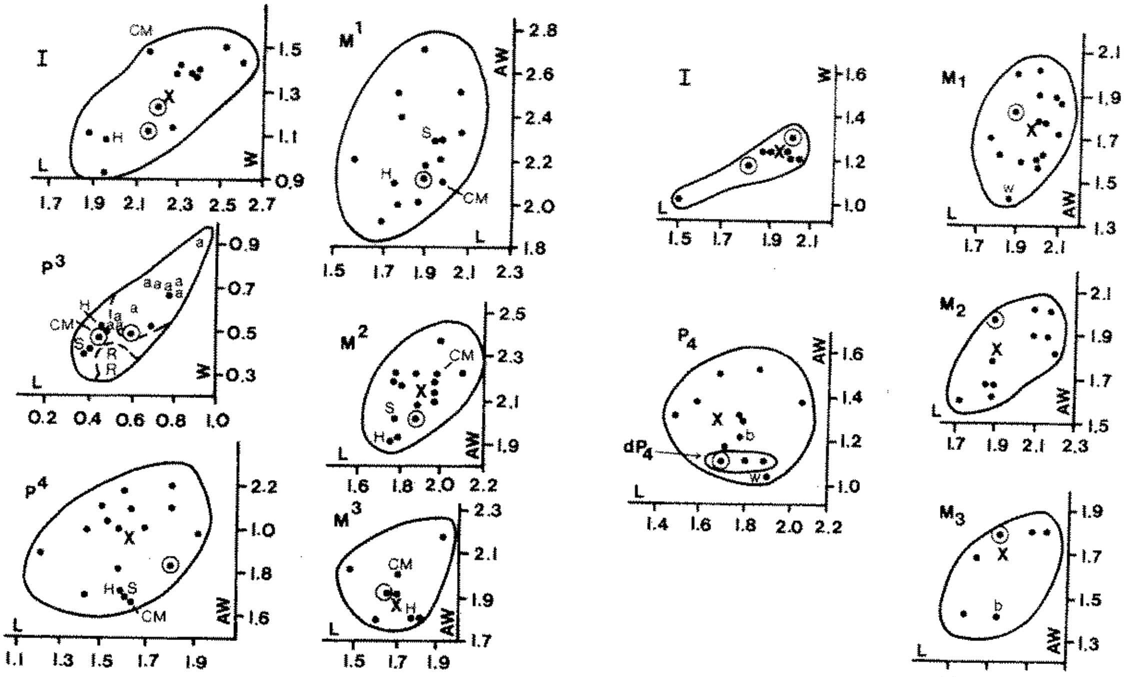

FIG. 10. Variation in tooth proportions is illustrated in these bivariate graphs (length by width or anterior width) of each tooth of *Protoptychus hatcheri*. All measurable specimens are included. ⊙ indicates FMNH skeleton; CM, Carnegie Museum specimen; H, *P. hatcheri* type; S, *P. smithi* type; X, mean; a, alveolar measure; r, root measure; b, broken; w, worn.

cept for its small size. Preservation is poor in the area, so that I have not been able to determine anything about the styloid process. The ulna has a short olecranon and tight semilunar notch about equal to the length of the olecranon; its shaft is gently curved (figs. 3–5). To date no specimen preserves the manus, which presumably was correspondingly delicately proportioned.

PELVIC GIRDLE AND HIND LIMB—Here we come to the remarkable enlargement of the girdle and especially the hind limb, which in comparison with most rodents is a noteworthy feature. Each of the three skeletons contributes to our understanding in a different way. PM 39371 is the most complete overall, PM 8018 has the most complete tarsus, and CM 9386 affords the best opportunity for examination of the joints and medial aspect of various elements. The ilia flare apart anteriorly and receive the transverse processes of the sacral vertebrae. Pubes are rather small with an elongate symphysis (well exposed in PM 39371, fig. 4). Ilia and ischia are stouter, and the acetabulum is also stout and well buttressed by all three elements. The femur is long and relatively slender; its head and greater and lesser trochanters are large. The third trochanter is narrow and elongate, and is situated about as far below the lesser as that trochanter is beneath the near-spherical head. The neck is short but distinct. The shaft is quite straight and the distal condyles are prominent. Tibia and and fibula are both very elongated as can be seen on CM 9386 (fig. 5D) and PM 39371 (fig. 4). The fibula is a straight slender strut with expanded proximal (complete only on PM 39371) and distal articular ends. Shafts of the two bones are separated from one another for about two-thirds of their length proximally, united distally. That of the tibia is stout, slightly sinuously curved so that in the proximal half the anterior edge is convex, in the distal half concave. The proximal articulation is triangular with facets for lateral and medial condyles. There is a prominent cnemial crest.

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FIG. 9. A–I, A series of mandibles of *Protoptychus hatcheri* showing variations in the population. Specimens shown are: **A,** PM 8009. **B,** PM 8010. **C,** PM 8006. **D,** PM 8011. **E,** PM 2301. **F,** PM 2323. **G,** PM 2312. **H,** PM 2319. **I,** PM 2324. All are shown approximately ×6.

TABLE 5. Measurements (in cm) of limb and girdle elements of *Protoptychus* and some modern ricochetal rodents.

| | *Protoptychus* | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | CM 9386 | PM 8018 | PM 39371 | PM 2088 | PM 2091 | PM 2092 | PM 2094 | PM 8013 |
| Pectoral girdle and limb | | | | | | | | |
| Total articulated length | — | ~5.5 without manus | ~5.0 | — | — | — | — | — |
| Scapula | | | | | | | | |
| Length | — | 2.05 | ~1.93 | — | — | — | — | — |
| Greatest width | — | 0.87 | — | — | — | — | — | — |
| Spine to anterior edge | — | 0.31 | — | — | — | — | — | — |
| Spine to posterior edge | — | ~0.55 | — | — | — | — | — | — |
| Humerus | | | | | | | | |
| Length | — | 1.77 | 1.76 | — | — | — | — | — |
| Proximal width | — | 0.35 | ~0.35 | — | — | — | — | — |
| Distal width | — | ~0.4 | >0.26 | 0.35 | — | — | — | — |
| Radius length | >1.78 | 1.91 | >>1.16 | — | — | — | — | — |
| Ulna length | >2.28 | 2.35 | >>1.55 | — | — | — | — | — |
| Length olecranon process | ~0.35 | ~0.36 | ~0.27 | — | 0.22 | — | — | — |
| Length of articulation | ~0.25 | ~0.20 | 0.18 | — | 0.17 | — | — | — |
| Carpus, metacarpus, manus length | — | — | — | — | — | — | — | — |
| Pelvic girdle and limb | | | | | | | | |
| Total articulated length (il–pes) | — | — | e>12.00 | — | — | — | — | — |
| (fem–pes) | — | e>12.00 | e>10.60 | — | — | — | — | — |
| Pelvis length | — | — | 3.54 | — | — | — | — | — |
| Ilium length | — | — | 1.80 | — | — | — | — | — |
| Femur | | | | | | | | |
| Length | — | — | 3.37 | — | — | — | — | — |
| Greatest proximal diameter (head to trochanter) | 0.80 | — | >0.72 | — | — | ≥0.77 | >0.70 | — |
| Distal width | ~0.69 | * | ~0.58 | — | — | — | — | — |
| Tibia/fibula length | 4.87 | 4.52 | 4.31 (4.34) | — | — | — | — | — |
| Tarsus, metatarsus, pes length | — | 4.72 | — | — | — | — | — | — |
| Retroproc. calcaneum | 0.63 | 0.52 | 0.55 | — | — | — | — | — |
| Metatarsals | 1.94 | 1.99 | ≥1.91 | — | — | — | — | — |
| Sacrum | | | | | | | | |
| Length (2 vert) | 0.92 | — | >0.84 | — | — | — | — | 0.87 |
| (3 vert) | 1.44 | — | — | — | — | — | — (2+) | 1.14 |
| (5 vert) | — | — | — | — | — | — | — | — |
| Maximum width (or half width ×2) | 1.25 | — | 1.32 | — | — | — | — | 1.28 |
| Tail length | >>5.50 | — | — | — | — | — | — | — |

e, estimate. Tail length of CM 9386 is the measure of the articulated four caudals and two partial caudals from the midsection, about #11 to #17, plus two more posterior caudals.

TABLE 5. Continued.

| | *Protoptychus* | | | | | | | Comparative specimens | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | *Jaculus blanfordi* | |
| | PM 8017 | PM 39825 | PM 39838 | Range | | N | Mean | FM 97692 | FM 97693 |
| | | | | Min. | Max. | | | | |
| Pectoral girdle and limb | | | | | | | | | |
| Total articulated length | — | — | — | ~5.0 | ~5.5 | 2 | ~5.25 | *>4.95 | *>5.40 |
| Scapula | | | | | | | | | |
| Length | — | — | — | 1.93 | 2.05 | 2 | 2.00 | 1.36 | 1.49 |
| Greatest width | — | — | — | 0.87 | | 1 | 0.87 | 0.80 | 1.00 |
| Spine to anterior edge | — | — | — | 0.31 | | 1 | 0.31 | 0.21 | 0.29 |
| Spine to posterior edge | — | — | — | ~0.55 | | 1 | 0.55 | 0.64 | 0.76 |
| Humerus | | | | | | | | | |
| Length | — | — | — | 1.76 | 1.77 | 2 | 1.77 | 1.27 | 1.39 |
| Proximal width | — | — | — | 0.35 | | 2 | 0.35 | 0.36 | 0.39 |
| Distal width | — | — | — | 0.40 | 0.35 | 2 | 0.38 | 0.43 | 0.44 |
| Radius length | — | — | — | 1.91 | | 1 | 1.91 | 1.59 | 1.88 |
| Ulna length | — | — | — | 2.28 | 2.35 | 2 | 2.32 | 1.97 | 2.25 |
| Length olecranon process | — | — | — | 0.22 | 0.36 | 4 | 0.30 | 0.28 | 0.31 |
| Length of articulation | — | — | — | 0.17 | 0.25 | 4 | 0.20 | 0.18 | 0.16 |
| Carpus, metacarpus, manus length | — | — | — | — | | 0 | — | *>0.89 | *>0.84 |
| Pelvic girdle and limb | | | | | | | | | |
| Total articulated length (il–pes) | — | — | — | — | | 0 | — | | 15.49 |
| (fem–pes) | — | — | — | — | | 0 | — | 12.94 | 13.94 |
| Pelvis length | — | — | — | 3.54 | | 1 | 3.54 | 2.58 | 3.48 |
| Ilium length | — | — | — | 1.80 | | 1 | 1.80 | 1.37 | 1.68 |
| Femur | | | | | | | | | |
| Length | — | — | — | 3.37 | | 1 | 3.37 | 2.95 | 3.46 |
| Greatest proximal diameter (head to trochanter) | — | — | — | 0.70 | 0.80 | 4 | 0.75 | 0.69 | 0.79 |
| Distal width | 0.64+ | 0.62 | 0.69 | 0.58 | 0.69 | 5 | 0.64 | 0.49 | 0.59 |
| Tibia/fibula length | — | — | — | 4.31 | 4.87 | 3 | 4.51 | 4.81 | 5.34 |
| Tarsus, metatarsus, pes length | — | — | — | 4.72 | | 1 | 4.72 | *>6.17 | *>5.97 |
| Retroproc. calcaneum | — | — | — | 0.52 | 0.63 | 3 | 0.57 | 0.56 | 0.70 |
| Metatarsals | — | — | — | >1.91 | 1.99 | 3 | 1.96 | 3.61 | 3.77 |
| Sacrum | | | | | | | | | |
| Length (2 vert) | — | — | — | >0.84 | 0.92 | 3 | 0.88 | 0.59 | 0.69 |
| (3 vert) | — | — | — | 1.44 | | 1 | 1.44 | 0.87 | 1.05 |
| (5 vert) | — | — | — | — | | 0 | — | 1.46 | 1.85 |
| Maximum width (or half width ×2) | — | — | — | 1.25 | 1.32 | 3 | 1.28 | 0.80 | 1.01 |
| Tail length | — | — | — | >>>5.50 (e×3 or ×4)<br>(e based on a length 3× or 4× segment present) | | 1 | e16–22 | *>15.77 | *>22.09 |

* Element present but too buried in matrix to measure, or within skin.

TABLE 5. Continued.

| | Comparative specimens | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | *Jaculus j. flavillus* | | *Allactaga tetradactyl* | *Dipodomys microps occidentalis* | *Dipodomys merriami* | | *Dipodomys deserti* | *Dipodomys* sp. |
| | **FM 84620** | **FM 98937** | **FM 78616** | **FM 123328** | **FM 54757** | **FM 55678** | **FM 47934** | **FM 34917** |
| Pectoral girdle and limb | | | | | | | | |
| Total articulated length | ~6 | — | — | >5.62 | — | 4.40 | 5.08 | 6.36 |
| Scapula | | | | | | | | |
| Length | 1.47 | — | 1.34 | 1.65 | 1.42 | 1.43 | 1.48 | 1.90 |
| Greatest width | 1.05 | — | 0.80 | 1.10 | 0.79 | 0.86 | 0.85 | 1.30 |
| Spine to anterior edge | 0.24 | — | 0.22 | ~0.29 | 0.18 | 0.23 | 0.19 | 0.29 |
| Spine to posterior edge | 0.79 | — | 0.69 | ~0.80 | 0.63 | 0.63 | 0.68 | 1.08 |
| Humerus | | | | | | | | |
| Length | 1.49 | — | 1.19 | 1.55 | — | 1.19 | 1.28 | 1.84 |
| Proximal width | ~0.46 | — | 0.28 | 0.36 | — | 0.31 | 0.32 | 0.46 |
| Distal width | 0.48 | — | 0.36 | 0.42 | — | 0.38 | 0.41 | 0.57 |
| Radius length | 1.86 | — | — | 1.82 | 1.62 | 1.60 | 1.59 | 2.28 |
| Ulna length | 2.14 | * | — | 2.18 | 1.87 | 1.87 | 1.93 | 2.66 |
| Length olecranon process | ~0.40 | — | — | 0.30 | 0.22 | 0.20 | 0.23 | 0.29 |
| Length of articulation | ~0.19 | ~3.34<br>(as skin) | — | ~0.18 | 0.14 | 0.15 | 0.14 | 0.21 |
| Carpus, metacarpus, manus length | ~1.25 | *<br>olec. to tip of manus | — | 1.01 | 1.01 | 0.94 | 1.05 | 1.45 |
| Pelvic girdle and limb | | | | | | | | |
| Total articulated length (il–pes) | ~16.60 | — | — | >11.27 | 10.02 | 10.17 | >9.37 | 14.68 |
| (fem–pes) | ~14.90 | — | — | >8.93 | 8.84 | 8.92 | >7.97 | 12.24 |
| Pelvis length | 3.44 | — | 2.28 | 3.27 | 2.61 | 2.63 | 2.74 | 4.17 |
| Ilium length | 1.90 | — | 1.11 | 1.80 | 1.52 | 1.47 | 1.61 | 2.37 |
| Femur | | | | | | | | |
| Length | 3.64 | — | b>2.74 | 2.85 | 2.49 | 2.44 | 2.58 | 3.57 |
| Greatest proximal diameter (head to trochanter) | 0.80 | — | 0.60 | 0.58 | 0.52 | 0.45 | 0.56 | 0.92 |
| Distal width | 0.63 | — | b | 0.49 | 0.39 | 0.37 | 0.42 | 0.65 |
| Tibia/fibula length | 5.54 | — | — | 3.79 | 3.44 | 3.36 | 3.37 | 5.15 |
| Tarsus, metatarsus, pes length | 6.90 | ~6.10<br>(as skin) | — | 4.02 | 3.44 | 3.56 | 3.54 | 5.32 |
| Retroproc. calcaneum | 0.51 | — | — | 0.34 | 0.52 | 0.27 | 0.31 | 0.50 |
| Metatarsals | 4.24 | — | — | 1.79 | 1.59 | 1.59 | 1.60 | 2.15 |
| Sacrum | | | | | | | | |
| Length (2 vert) | 0.64 | — | 0.52 | 0.66 | 0.55 | 0.51 | 0.53 | 0.84 |
| (3 vert) | 1.00 | — | — | — | — | — | 1.19 (4) | 3.08 (7) |
| (5 vert) | — | — | 1.16 | 1.68 | 1.32 | 1.34 | — | 2.26 |
| Maximum width (or half width × 2) | 0.89 | — | 0.79 | 0.93 | 0.70 | 0.78 | 0.82 | 1.30 |
| Tail length | *>19.53 | ~18.40<br>(as skin) | *>17.22 | e16.15<br>>14 as skin | >10.73 | — | 11.33 | 20.70 |

* Element present but too buried in matrix to measure, or within skin; e, estimate; b, broken.

TABLE 6. Status of vertebrae and ribs of specimens of *Protoptychus*.

| Vertebra number | PM 8013 | PM 8018 | | | PM 39834 | PM 39371 | | | CM 9386 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | vertebra | Left rib | Vertebra | Right rib | vertebra | Left rib | Vertebra | Right rib | Left rib | Vertebra | Right rib |
| Cervical | | | | | | | | | | | |
| 1 | | | X | | | | X | | | — | |
| 2 | | | X | | | | X | | | — | |
| 3 | | | b | | | | b | | | — | |
| 4 | | | b | | | | b | | | — | |
| 5 | | | b | | | | b | | | — | |
| 6 | | | b | | | | b | | | — | |
| 7 | | | b | | | | b | | | — | |
| Thoracic | | | | | | | | | | | |
| 1 | | X | b | b | | b | b | X | — | — | — |
| 2 | | X | b | b | | b | b | X | — | — | — |
| 3 | | X | b | b | | b | b | X | — | — | — |
| 4 | | X | b | x | | b | b | X | — | — | — |
| 5 | | X | b | X | | b | b | X | — | — | — |
| 6 | | X | b | X | | b | b | X | — | — | — |
| 7 | | X | X | X | | b | b | X | — | — | — |
| 8 | | X | X | X | | b | b | X | — | — | — |
| 9 | | b | X | X | | b | b | X | — | — | — |
| 10 | | b | X | X | | b | b | — | — | — | — |
| 11 | | | X | | | | b | | | — | |
| 12 | | | X | | | | b | | | — | |
| 13 | | | X | | | | b | | | — | |
| Lumbar | | | | | | | | | | | |
| 1 | | | X | | | | b | | | — | |
| 2 | | | X | | | | b | | | X | |
| 3 | | | X | | | | X | | | — | |
| 4 | | | X | | | | X | | | X | |
| 5 | | | ? | | | | X | | | — | |
| 6 | | | ? | | | | X | | | X | |
| ?7 | | | ? | | | | X | | | X | |
| Sacral | | | | | | | | | | | |
| 1 | X | | — | | — | | X | | | X | |
| 2 | X | | — | | X | | X | | | X | |
| 3 | X | | — | | — | | ? | | | X | |
| ?4 | ? | | — | | — | | ? | | | ? | |
| Caudal | | | | | | | | | | | |
| 1 | | | — | | | | ? | | | X | |
| 2 | | | — | | | | ? | | | X | |
| 3 | | | — | | | | ? | | | X | |
| 4 | | | — | | | | — | | | X | |
| 5 | | | — | | | | — | | | X | |
| 6 | | | — | | | | — | | | X | |
| 7 to end | | | — | | | | X | | | —<br>—<br>plus 2 posterior, uncertain position | |

X, elements known to be preserved; x, those represented by an impression, or an unidentified bone in the expected position of the indicated element; b, buried but presumed to be present; —, missing element; ?, uncertainty as to whether or not a usual element is actually present in *Protoptychus*, or may be represented by a number larger than the usual number in rodents.

The six caudal vertebrae of CM 9386 were originally thought to be 1–6 but are now considered to be farther back in the tail, about 7–11.

The distal articular surfaces of both tibia and fibula are hidden, partly buried, and in articulation with astragalus and calcaneum. The astragalus is small and compact, the calcaneum also except that its tuberosity is quite large. The other tarsals are present, mostly in articulation, in all three skeletons. The metatarsus is enlarged, with all of the main toes involved, not just that of digit 3, which is only slightly longer and more massive than those of digits 2, 4, and 5. The pollex is shorter than the others, best seen in PM 8018, being about a third the length of the others. In this regard it differs from the condition of the most specialized of the species of *Jaculus,* in which the central metatarsal has taken over completely to become a functional cannon bone.

## Discussion

The many parallels of anatomical features between jerboas, kangaroo rats, and *Protoptychus* combine to define a distinctive life niche characterized by bipedal hopping and by marked directional changes. This ricochetal motion serves remarkably well as a means of escape from predators, and as far as we can tell the first rodent to develop these specializations was *Protoptychus* in late Middle Eocene time, about 44 to 45 million years ago (Berggren et al., 1985). Scott (1895) clearly recognized its hopping potentialities from the few, but significant, remains that he had: the skull with its enlarged and inflated bullae. Even lacking the postcranial skeleton he felt confident with his assignment of it as an ancestral form of the Dipodidae, possibly related to the ancestry of the Heteromyidae as well. Had he known the postcranial skeleton as we do now, doubtless that opinion would have been reinforced, for like the bullae, the limb and body proportions correspond very closely to those of modern kangaroo rats and jerboas. In them all the very greatly lengthened hind limb is the common feature. Differences among them result from which segment(s) of the limb are lengthened the most.

Wahlert (1973) succinctly reviewed the taxonomic history of *Protoptychus* to that date and in his detailed discussion he systematically considered possible relationships to a number of rodent groups, especially *Mysops* and others within the Paramyidae (*sensu lato*). He concluded that on cranial features and dental evidence *Protoptychus* could be ruled out of close relationship to any rodent except some paramyids and *Mysops* among the protrogomorphs, and caviomorphs. His argument for caviomorph ancestry is complex, and I think possible but rather unlikely. The problem is that assignment to a primitive group does not tell us much about where a line is headed, and there are no strong indications for relationship to any more specialized groups.

I wonder if it is not time to reconsider a relationship of *Protoptychus* to the Dipodidae as a possibility. I find no real conflict with having the Dipodidae arise from the Ischyromyidae (or Paramyidae) either directly or via the Sciuravidae (Wilson, 1949; Wood, 1959). It is easy to derive the dental morphology of *Protoptychus* from that of either family. The dental morphological gap came later. Clearly the dental evidence aligns *Protoptychus* with the Ischyromyoidea, the earliest and most generalized of the rodent groups (Wood, 1935, 1937, 1959), so why not bring the dipodid line from its protrogomorph ancestor through the Protoptychidae, as Scott (1895) originally suggested?

Wahlert (1973) dismissed any myomorph rodent relationship for *Protoptychus,* "because the cheek tooth cusp pattern is essentially different." Generally that is true, but in as much as the pattern in *Protoptychus* is only slightly evolved beyond that of the protrogomorphs, which has to have been the base for both *Protoptychus* and the myomorphs, that dismissal is not convincing to me. From my comparisons of the cheek teeth, I believe it possible to derive the *Jaculus* form from that of *Protoptychus.* Furthermore, Wahlert (1973) considered the stapedial artery to be absent, but I find its foramen precisely in the same position in *Jaculus* and *Protoptychus.* This evidence plus the fundamental similarity of the infraorbital foramen in both taxa, in addition to the apparently closely similar, highly specialized bullae and the shared saltatorially specialized body proportions, leads me to think that Scott's conclusion was probably correct as far as a dipodid relationship of *Protoptychus* is concerned. But his notion of a relationship to the Heteromyidae, or Schlosser's (1924) to the Geomyoidea have proven to be wrong: Wood (1935) discredited any close geomyoid relationship on dental evidence, and Wahlert (1973), by showing *Protoptychus* to be hystricomorphous to a degree, put to rest any notion of a sciuromorph relationship. From all of this I conclude that *Protoptychus* and its family belong within the Myomorpha in a position linking the portion of that group which contains the Dipodidae with its an-

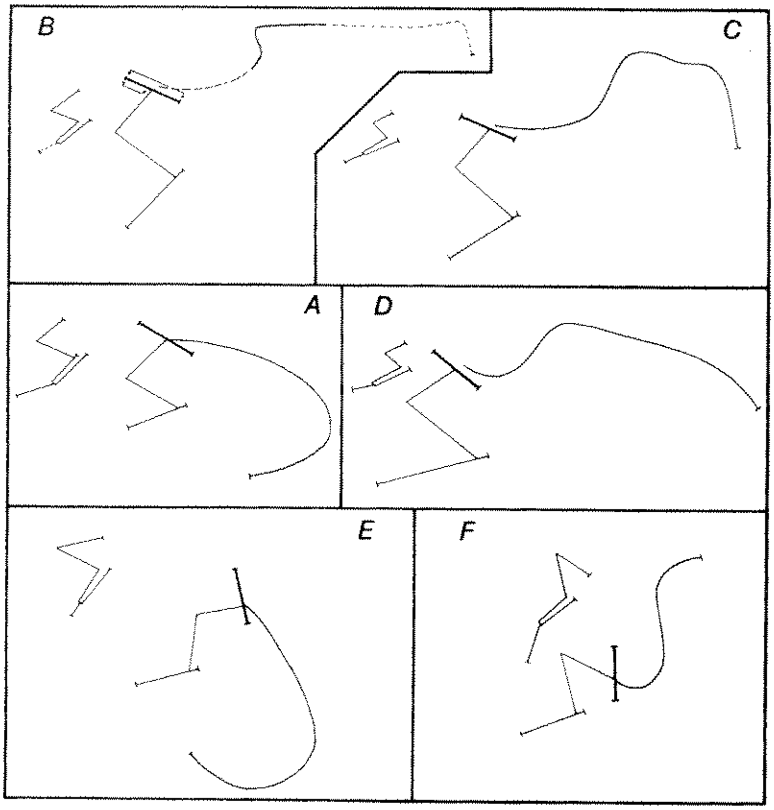

FIG. 11. Diagrammatic representation of limb and tail proportions in *Protoptychus* and some comparative specimens. An ancestral protrogomorph is shown in A, two modern highly specialized ricochetal forms in C and D, and two non-hopping, more generalized modern forms in E and F. **A,** *Paramys delicatus.* **B,** *Protoptychus hatcheri.* **C,** *Dipodomys* sp. **D,** *Jaculus blanfordi.* **E,** *Mus musculus* LAC gray strain. **F,** *Sciurus vulgaris.* Not to scale; instead adjusted so that all pelvic lengths are approximately equal.

cestral protrogomorph stock, somewhere within the Ischyromyoidea. Figure 12 expresses the general set of relationships of this conceptual framework. In Figure 12A the primitive, generalized protrogomorphous condition is shown to give rise to the various specialized conditions: sciuromorphous, hystricomorphous, and myomorphous. The degree to which the latter shares in developing the primary attributes (Zygomatic Plate and I.O.F.) is indicated by the overlapping patterns. In Figure 12B this is translated into a hypothetical phylogeny, modified from that presented by Wood in 1959.

## Conclusions

The anatomy, especially that of the jaws and most of the postcranial skeleton, is now known to a fair degree. Previously only the skull and upper dentition had been known. It suggests an agile animal with a ricochetal hopping gait. The skull with its enlarged infraorbital foramina is hystricomorphous at a myomorph level of expansion of that foramen, and the jaws are weakly hystricognathous. The dentition is closest to the condition in protrogomorphs. The auditory bullae are greatly expanded with three chambers visible externally: a large open mastoid chamber anterodorsally, another large open chamber posterodorsally and posteriorly that probably is formed by the exoccipital or possibly also by the mastoid, and an enlarged tympanic chamber proper. Sutures are indistinct so that one cannot be certain on this point. Details of the interior of the bullae are few. Other than the generally open condition of the two upper chambers, we cannot tell whether there are any septa other than the major ones visible from the exterior. These structures are all too small and delicate to permit further preparation.

Lumbar, sacral, and anterior caudal vertebrae

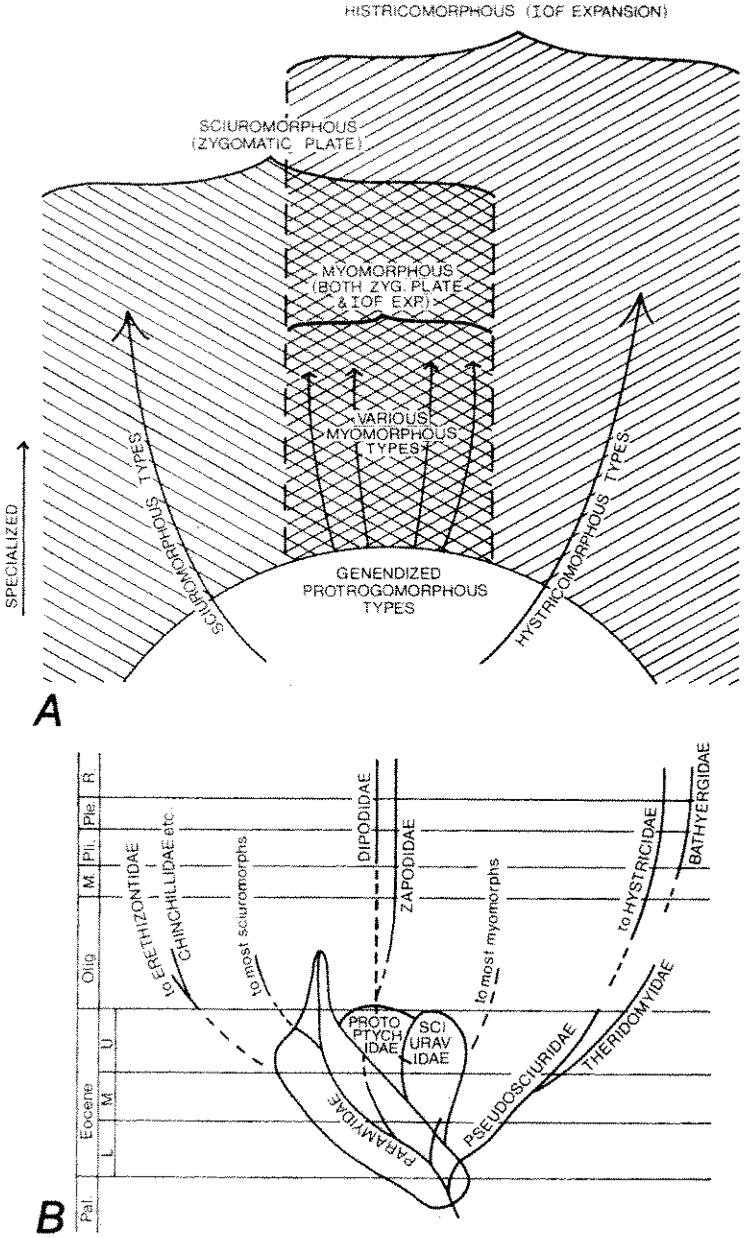

FIG. 12. **A,** Scheme illustrating the manner by which the generalized protrogomorphous condition of the primitive rodents gave rise to the three major specialized types: the sciuromorphous types specialized the zygomatic plate; the hystricomorphous types, the I.O.F. expansion; the myomorphous types used both features in varying degrees. **B,** Phylogenetic scheme to show the conception of probable interrelationships of *Protoptychus* and its family Protoptychidae to its presumed ancestral family Paramyidae, either directly or via family Sciuravidae, and to its myomorph descendants, the Dipodoidea.

are relatively expanded, as is the pelvic girdle. The hind limb is enlarged greatly, but the foot is five toed and generalized in most other respects. The systematic relationships remain somewhat doubtful, but I lean towards the position that the Protoptychidae is a myomorph family close to its Ischyromyoid (protrogomorph) ancestry, and that it lies on the line to the Dipodidae. This conclusion has but a few rigorous bases, and in several ways, particularly dentally, *Protoptychus* is sufficiently generalized that it cannot be precluded from being related to dipodids.

The animal is thus far known only from a very limited area geographically and chronostratigraphically: Uinta and Washakie Basins of Utah and Wyoming between 44 and 45 MY ago, about in middle Uintan time. Because all similar modern rodent analogues, whether related or convergent, are semiarid adapted, it is assumed that this one was too. Hence, I conclude that the divides between the drainages, and probably the general area as well, must have been rather arid. From the numerous associated faunal elements we can be certain that the major drainages leading into the basins from the higher surrounds supplied sufficient water to support a good riverine forest with its contained fauna.

## Acknowledgments

Over the past two decades I have had help with photography from John Baylis, Homer Holdren, and Fred Huismans, and most recently from Ronald Testa and his crews in the Field Museum Division of Photography. To this latter group I am especially indebted for the photographs in Figures 4, 6, and 7, and for prints used in most of the others.

My field crews have generally been small: Ronald Lambert and I worked together in 1959, the year of discovery of the locality and first skeleton. Crews on each subsequent year have spent from a few hours to a few days crawling over the outcrop to collect the many bits and pieces that compose the population sample. Those individuals who worked between 1960 and 1975 are listed in my 1978 report. Post-1975 field crews include, in addition to myself and Priscilla Turnbull (through 1985) and Hedy Turnbull (since 1986), Floyd Richie, John Flynn, and Karl Przedpelski in 1979; John Flynn, Ted Wallace, and Tom Przedpelski in 1980; and Robert Rosenberg, Tom Przedpelski, Kubet Luchterhand, and A. James Turnbull in 1981, most of whom have been involved in one way or another with collecting at the *Protoptychus* locality. Welcome support has come from Lois and Elza Eversole and their son John of the Eversole Ranch near the Basin center, and from the late Murray Daniels, his wife Mary Jane, and their family of Rawlins, who have often assisted in the field as well. Preparation has been minimal for the many fragmentary specimens, but for the two skeletons has been time consuming. I managed most of that on the first skeleton, and have had the patient and meticulous help of William Simpson for the superb job he did on the scrambled legs and other parts of PM 39371, the second skeleton. Without that help I could not have completed this study.

The Field Museum, through the Maurice Richardson Paleontological Fund, has supported the field work over these many years, and Rainer Zangerl, Edward Olsen, David Raup, and John Bolt have in their turn as Chairman of the Department of Geology given encouragement, each in his own way. To all of those listed above I give my sincere thanks for their help, most of all to my late wife, Priscilla, and now to Hedy, for their many and diverse ways of aiding with whatever task was in need of help, whether it was finding the specimen I had just crawled over, keeping the field camp, or correcting my grammar.

Finally, I wish to acknowledge the several colleagues that I asked to criticize the manuscript. Not being a specialist in rodent systematics, I am very appreciative of comments by A. E. Wood, M. Dawson, and J. Wahlert on the initial draft, and by M. Mason, P. Brylski, R. Wilson, and J. Flynn on later versions. I have attempted to respond to nearly all of their suggestions, which I am certain have greatly improved the work. Any differences from their views are my doings, of course, and are in no way their responsibility.

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## Appendix

The following materials are referred to *Protoptychus*:

PM 8018 and 39371 are the two nearly complete skeletons;
PM 2309, 2310, and 8003 are left premaxillae with I, (G82293);
PM 39833 is a right premaxilla with broken I;
PM 8015B, 37377, 39827, 39828, and 39839 are left upper incisors;
PM 39836 and 39895 are right upper incisors;
PM 8007 and 8008 are edentulous left maxillae with alveoli or roots of P$^{3}$–M$^{3}$;
PM 37381 and 39824 are edentulous left maxillary fragments with roots of P$^{3-4}$;
PM 39893 is a left maxillary fragment with P$^{4}$–M$^{2}$, and the alveolus of P$^{3}$;
PM 2084 and 39894 are left maxillary fragments with P$^{4}$–M$^{1}$;
PM 2303 consists of a left M$^{1-2}$, (G82303);
PM 2306 and 2322 are left maxillary fragments with P$^{4}$–M$^{2}$ and alveolus of P$^{3}$, the last with alveolus of M$^{3}$, (G82301);
PM 2304, 2325, and 8029 are left maxillae with P$^{4}$–M$^{3}$, root of P$^{3}$, except the last which has alveolus of P$^{3}$, (G81974, G82298);
PM 37373 is a left maxillary fragment with M$^{2-3}$, roots of M$^{1}$;
PM 2302 is an edentulous right maxilla with alveoli of P$^{3}$–M$^{1}$;
PM 2307 is a right maxillary fragment with P$^{3}$–M$^{1}$;
PM 2321 and 39898 are right maxillary fragments with P$^{4}$ and alveoli of P$^{3}$ and M$^{1}$, (G82274);
PM 8004 is a right maxillary fragment with P$^{4}$–M$^{2}$, root of P$^{3}$;
PM 37382 is a right maxilla with P$^{3}$–M$^{3}$;
PM 37384 is a right maxilla with broken P$^{3}$, and with P$^{4}$–M$^{2}$;

PM 37385 is a right maxilla with $P^4$–$M^3$, alveolus of $P^3$;
PM 2301 and 2324 are left ramus fragments with $P_4$–$M_1$, broken I, alveoli of $M_2$, (G81967);
PM 2305 and 2323 are left ramus fragments with $P_4$–$M_1$, (G81991);
PM 2319 is a left mandibular ramus with $M_{1-3}$, broken I, (G81976–G81978);
PM 8009 is a left mandibular ramus with I, $P_4$–$M_3$;
PM 8010 is a left mandibular ramus with broken I, $P_4$–$M_2$;
PM 39829 is a left ramus fragment with broken $M_1$ and $M_{2-3}$;
PM 37374 is an edentulous left ramus fragment with alveoli of I, $P_4$–$M_1$;
PM 8015A is a partial lower I;
PM 8016 is the anterior half of a left lower molar;
PM 2312 is a right ramus fragment with $P_4$–$M_1$, (G81972);
PM 8006 is a right ramus fragment with $P_4$–$M_3$;
PM 8011 is a right ramus fragment with I, $P_4$–$M_1$;
PM 37375 is a right ramus fragment with $M_{1-2}$, alveoli of $M_3$;
PM 39832 and 39896 are right mandibular rami with I, $P_4$–$M_2$, the latter with alveolus of $M_3$;
PM 8005 is a right ramus fragment with $M_{2-3}$;
PM 39830 is a right ramus fragment with $P_4$–$M_2$;
PM 2326 is a right ramus fragment with $P_4$;
PM 39831 consists of a right $P_4$–$M_1$;
PM 2100 is a right $M_1$;
PM 37376 is a right lower molar, probably $M_3$;
PM 2088 is the distal end of a humerus;
PM 39835 is the proximal ⅔ of a radius;
PM 2091 is the proximal end of an ulna;
PM 2092 and 2094 are proximal ends of femurs;
PM 8017, 39825, and 39838 are distal ends of femurs;
PM 39837 is a fragment of a femur;
PM 8013 is a partial sacrum;
PM 39834 is a sacral vertebra.