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## *PROHYRACODON ORIENTALE* KOCH, THE OLDEST KNOWN TRUE RHINOCEROS

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The evolutionary significance of *Prohyracodon orientale* Koch (not to be confused with *Prothyracodon* Scott and Osborn), an Eocene true rhinoceros, has usually been overlooked. The only known material is from Eocene variegated clays of Transylvania (formerly Hungarian, now Rumanian territory). This neglect has been caused partly by its being represented only by fragmentary material in the somewhat isolated University of Cluj, and more by Koch's indistinct figures (1897), on which Abel (1910) based his slightly less satisfactory composite figure. In addition, there has been skepticism as to the extreme antiquity assigned to it. Koch, as indicated by his unfortunate name, considered the cursorial rhinoceros *Hyracodon* (Hyracodontidæ) its closest relative, though he also saw resemblances to *Aceratherium occidentale* and *Hyrachyus*. Abel, however, referred it correctly to the true rhinoceroses. While studying the earlier European fossil rhinoceroses, in the various European museums, I was permitted, through the courtesy of Professors Voitesti, Stanciu, and Mateescu, to restudy Koch's types, and was enabled to obtain one of the third upper molars by exchange (that shown by Koch, 1897, Pl. XII, fig. 2). It is now No. 21935 in the American Museum of Natural History (Fig. 5). This present study was originally included in the scope of a projected paper on the evolutionary lines of European rhinoceroses in general, but the considerable delay, before the remainder of the material will be in final shape for publication, makes it seem desirable to excerpt the data relating to *Prohyracodon*, making it generally available through separate publication. I wish to acknowledge the kindness of Dr. Florence Dowden Wood, who subordinated her own interests, during most of this trip, to act as my artist.

Koch collected the specimens about 1882 under the auspices of the Siebenbürgisches Museum, a Magyar learned society of Klausenburg. As yet this society has no building of its own, so the specimens are distributed, for the present, through the appropriate University collections. Fossils are in the Geological and Mineralogical Institute of the

University of Cluj. There is no relationship with the Siebenbürgisches Museum at Hermannstadt (=Sibiŭ), which is a general museum under Saxon auspices. The Oligocene rhinoceros, from a higher level, which Koch (1911) figured as "*Præaceratherium minus*" (actually *Ronzotherium* [=*Paracænopus*] *filholi*), as well as the types of *Prohyracodon orientale* Koch (1897), are in Cluj. The type of the early titanothere, *Brachydiastematherium transsylvanicum*, from the same level, is at Budapest, however, in the Museum of the Hungarian Geological Survey. There are only a few fragments at Cluj which were found later by Koch. Koch's locality is a ravine beside Andrashaza Hill near the town of Mera, a few kilometers west of the city of Cluj (otherwise known as Klausenburg, in German, and Kolozsvár, in Magyar). The locality can be seen from the train window, to the north of the Budapest-Cluj line.

The geologic age of its horizon (Koch's Obere bunte Tonschichten) has been a subject of dispute. Koch (1894) described the stratigraphy of these beds in detail, giving extensive faunal lists for the various fossiliferous levels. He discussed the discovery of this rhinoceros-like form, which he compared to *Quercytherium* Filhol. *Prohyracodon orientale* and the peculiar titanothere, *Brachydiastematherium transsylvanicum* Böckh and Matyasovszky are the only mammals known from this horizon, which is, however, preceded and followed by marine invertebrate faunas in the Untere and Obere Grobkalkschichten. Koch interpreted its age as Middle Eocene, as he regarded both marine faunas as Middle Eocene. Stehlin (1903) doubted this on the basis of the progressiveness of *Prohyracodon*, and suggested the Oligocene as more reasonable, as did Matthew (1915). Abel, in his redescription of *Prohyracodon* (1910), illustrated with a composite of Koch's figures, reserved final judgment as to the age, though inclined to accept Koch's interpretation. The Hungarian Geological Survey informs me (letter, 1925) that, so far as they know, Koch's age determination is still valid, and Professor Mateescu, of the University of Cluj, who is making a careful study of the stratigraphy of the whole region, informs me in a letter dated August 12, 1928, that "So far, according to my results, I can not say otherwise than that the variegated beds of Andrashaza (Mera) belong to the Middle Eocene-Auversian." On this basis, then, *Prohyracodon* would be roughly equivalent in age to the Bridger of Wyoming, and would be at least as old as the oldest known American true rhinoceros (*Eotrigonias petersoni* Wood, 1927), and exceeded in age, among known rhinocerotoids, only by the Lost Cabin (Lower Eocene) representative of *Hyrachyus*. Certainly in view of the extensive invertebrate faunas above and below, there is not much likelihood that its age has been seriously misjudged.

In addition to teeth, various associated rhinocerotoid leg bones, presumably of the same species, were collected. The following teeth were present: two isolated $RM^3$s (Fig. 5); part of a right maxillary with broken $M^3$, and another part with broken $M^{1-2}$ (Fig. 4); a left maxillary with $M^3$, broken $M^2$, roots of $M^1$ and place for $P^4$ (Fig. 3), also the associated $LP^4$ (Fig. 2) and a $LP^3$, isolated (Fig. 1). The three $RM^3$s show the presence of at least three individuals, all young mature to mature. To avoid any possible future difficulties, I hereby select, as lectoholotype, the left maxilla with $M^{2-3}$ on which $P^4$ seems to fit and with which it is almost certainly associated, and $P^3$ very probably (Figs. 1–3). Koch's first discussion (other than casual mention) of this material (1894) indicates that the five left cheek-teeth ($P^3$-$M^3$) belong together, that the right molars ($M^{1-3}$) also belong together, and that all these teeth were found at the same time, the isolated $M^3$s being found later. The right molars may well be associated with the left cheek-teeth, as they show about the same degree of wear. The other original cotypes then become lectoparatypes.

Koch's figures, though accurate enough, are indistinct, and do not represent the specimen satisfactorily, except to one who has already seen it. By cleaning the remaining matrix from $LP^3$, $LP^4$, $RM^{1-2}$, and $LM^{2-3}$, I exposed various additional characters for the first time. These characters are indicated in figures 1–5, on which it is now possible to base a more accurate composite drawing (Fig. 6).

The animal is a true rhinoceros, of the "American" type, that is, the molar protocones are not constricted off from the protoconules as in most European rhinoceroses. It is primitive compared with most forms, but not extraordinarily so. The teeth are a little smaller than those of *Eotrigonias rhinocerinus*. The parastyles of $P^3$, $P^4$ and $M^3$ (the only teeth in which they are preserved) are of normal rhinocerine proportions and are plastered against the paracones. The premolars are primitive, with the median valley opening to the rear, and are already more advanced than in *Eotrigonias rhinocerinus* from the Uinta, since the metalophs are already rather prominent. These teeth are roughly comparable in evolutionary stage with the more primitive species of *Trigonias* and of *Cænopus* from the American Oligocene. The third upper molar has already lost all but a trace of the posterior buttress, and is more progressive than in some later rhinoceroses.

$P^3$ (Fig. 1) is subquadrate. The hypocone is incipiently defined from the protocone by grooves on both slopes of the ridge. The dentine of the protoloph has not yet become confluent with that of the ectoloph

at this stage of wear. The internal swell of the paracone may be called a crista, or not, according to taste. The long metaconule abuts against the buccal side of the hypocone, with only a minute "wind gap" to the rear left at this stage of wear. A groove runs down posteroexternally from it to the cingulum. A very little additional wear would have isolated the median valley as a medifossette. Slight grooves separate the parastyle, paracone, and metacone, on the outer slope of the ectoloph. There is a faint external cingulum between the paracone and metacone. Near the parastyle, the anterior cingulum seems to have been worn away by the high protoconid of $P_3$. From there, the cingulum swings up onto the protocone and stops. The internal cingulum starts at a level nearer the gum, and swings around to the rear of the tooth as the posterior cingulum.

Fig. 1. *Prohyracodon orientale* Koch, left $P^3$, apparently associated with lectoholotype, ×1, Geol. Min. Inst., Cluj.

MEASUREMENTS OF TYPES OF *Prohyracodon orientale* KOCH IN CLUJ

| | R | L |
|---|---|---|
| $M^{1-3}$, A–P | $^{k}55.0$ | $^{e}52.0$ |
| Width $P^3$ | | 17.0 |
| Length $P^4$ | | 13.4 |
| Width $P^4$ | | 18.4 |
| Length $M^1$ | | $^{e}15.0$ |
| Length $M^2$ | 19.3 | $^{e}18.8$ |
| Length $M^3$ | 19.0 | 19.8 |
| Width $M^3$ | | 19.8 |
| Length tibia | $^{k}195.0$ | |
| Length radius | | $^{k}175.0$ |
| Length radius (second individual) | | $^{k}165.0$ |

$^{e}$ = estimated.
$^{k}$ = fide Koch.

$P^4$ (Fig. 2) is much like $P^3$ in general plan, but is a little more differentiated. The tooth evidently erupted with the ectoloph rotated to the rear at a ninety-degree angle, and with the crown on the bias, as the ectoloph is badly worn, whereas there is progressively less wear toward the lingual side of the tooth, the protocone being absolutely unworn. In addition, there is a triangle of wear on the outer slope of the ectoloph which touches the base of the paracone and spreads out over the metacone, and which, obviously, could not have developed with normal

occlusion. The outline of $P^4$ is typical of a primitive rhinoceros, being rounded postero-internally, so that its shape is between subtriangular and subquadrate. The protoloph originally projected higher than the metaloph. An incipient hypocone is demarcated from the protocone, very slightly on the internal slope of the protoloph, and more definitely on the external slope. A crista is present. The metaconule forks internally, one fork abutting against the "hypocone," and the other pointing postero-internally. The anterior fork closes the median valley high up (3.5 mm. above the deepest part of the medifossette pit). The "wind gap" which is left leading from the median valley to the rear is about 2.5 mm. deep. From the "wind gap" a deep groove runs down toward the cingulum and disappears in a slight pit, opposite the end of the posterior fork of the metaconule. The medifossette is very deep, and a moderate postfossette is present. The parastyle, paracone and metacone are defined by slight grooves on the external slope of the ectoloph. A trace of an external cingulum appears on the rear of the metacone. There is a slight accessory cingulum on the anterior of the parastyle, near the base. The anterior cingulum, after forming a hump nearly opposite the protoconule, rises and ends against the sharp, nearly right angle, formed by the curve of the protoloph. The


Fig. 2. *Prohyracodon orientale* Koch, left $P^4$, almost certainly associated with lectoholotype, ×1, Geol. Min. Inst., Cluj.

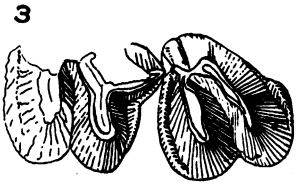



Fig. 3. *Prohyracodon orientale* Koch, left $M^{2-3}$. lectoholotype, ×1, Geol. Min. Inst., Cluj.

Fig. 4. *Prohyracodon orientale* Koch, right $M^{1-2}$, perhaps associated with lectoholotype, ×1, Geol. Min. Inst., Cluj.

internal cingulum starts at the other side of this angle, and after rising into the usual hummock at the posterointernal corner of the tooth, continues as the posterior cingulum.

No characters of $M^1$ can be deciphered, except the absence of any internal cingulum (Fig. 4).

$M^2$ is a typical primitive rhinoceros molar, of the American type (Figs. 3–4). The protocone is slightly defined posteriorly by a groove, adjoining which is a slight antecrochet. There is no crista. There is no internal cingulum, but anterior and posterior cingula are present.

All four $M^3$s are strikingly alike (Figs. 3 and 5). They are all triangular. At their several stages of wear, the dentine of the protoloph is confluent with that of the ectoloph on one tooth, obscured in one by a break, and not yet confluent in the other two. The protocone is not demarcated at all. A slight antecrochet is present. The parastyle is of normal rhinocerine type, with a sharp antero-exterior angle, and a very slight cingulum down the edge. Three of these teeth have a faint trace of a posterior buttress, which is absent altogether on the fourth (Fig. 3, Koch 1897). There is an anterior cingulum, a weak internal cingulum across the median valley, and a posterior cingulum which rises into a pronounced cuspule at the postero-external corner of the tooth. From here a very tenuous external cingulum continues nearly to the paracone.

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Fig. 5. *Prohyracodon orientale* Koch, right $M^3$, lectoparatype, ×1, Amer. Mus. Nat. Hist. No. 21935.

$M^3$ is somewhat suggestive of *Epitriplopus uintensis* (Peterson); the other teeth—$P^{3-4}$ and $M^2$—are totally different. It seems highly improbable that the Cluj species is closely related to any hyracodont;

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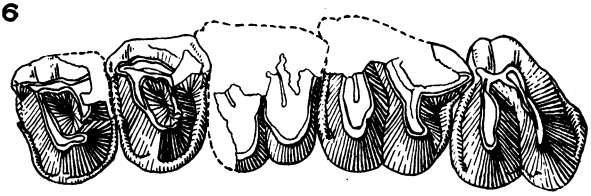

Fig. 6. *Prohyracodon orientale* Koch, left $P^3$–$M^3$, ×1, composite.

it suggests the upper Oligocene *Meninatherium telleri* of eastern Carniola (formerly in Austria, now in Jugo-Slavia), as Abel pointed out, and *Eotrigonias rhinocerinus* of Utah (Wood, 1927), among animals of comparable size. It is not close to *Cænolophus* or to *Ardynia* of Mongolia, or to any of the Hyrachyidæ.

From a morphological viewpoint, it is more suggestive of the American rhinoceroses than of the later typical European forms. Perhaps the

closest comparison is with *Eotrigonias rhinocerinus*, and after that, with *Meninatherium telleri*, but the genus *Prohyracodon* is isolated at present, both in time and in space. Its Eocene age and morphological progressiveness suggest strongly that the common ancestor of all lines of rhinoceroses and near-rhinoceroses must be looked for in formations not younger than Lower Eocene, and possibly as old as the Paleocene.

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