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A Primitive Rhinoceros from the Late Eocene of Mongolia[1]

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Up to the present time, only three genera, including five species, of Eocene true rhinoceroses have been reported throughout the world. Hence a partial skull carrying true rhinoceros cheek teeth but with a primitive perissodactyl incisor-canine region is an important addition to this handful of inadequately known forms.

The illustrations for the present paper were prepared by the late Mr. John C. Germann and Dr. Florence D. Wood. When available, right and left sides of the type specimen have been taken into consideration to make the illustrations as complete as possible, without calling attention to breaks or cracks at the expense of anatomical characters.

The abbreviation A.M.N.H. refers to the American Museum of Natural History.

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CLASS MAMMALIA

ORDER PERISSODACTYLA

FAMILY RHINOCEROTIDAE

SUBFAMILY FORSTERCOOPERIINAE, NEW TERM (= FORSTERCOOPERIDAE KRETZOI, 1940)

Pappaceras confluens, new genus and new species[1]

Figures 1, 2

TYPE: A.M.N.H. No. 26660 (field no. 915), front half of the skull and complete lower jaw, with most of the teeth and remaining alveoli, totaling a full placental series; collected September 16, 1930, by Liu Ta Ling, of the American Museum Central Asiatic Expedition of 1930.

HORIZON AND LOCALITY: Upper gray clays (well up, a little below the Houldjin contact), ?Irdin Manha Formation, late Eocene, 10 miles southwest of Camp Margetts, Iren Dabasu region, Inner Mongolia (for map, see Granger and Gregory, 1943, fig. 1, p. 350).

REFERRED SPECIMENS: A.M.N.H. No. 26666, a left ramus of the mandible, and A.M.N.H. No. 26667, a loose P^2; both presumably from the ?Irdin Manha Formation, Camp Margetts area, Mongolia.

GENERIC AND SPECIFIC CHARACTERS: Large for an Eocene rhinoceros, size of *Hyrachyus grandis* Peterson, smaller than *Subhyracodon occidentalis;* hornless; snout of primitive perissodactyl type; nasals, nasal incision, premaxillaries, and frontals of *Hyrachyus* aspect; face long and fairly deep; lower jaw resembling that of *Trigonias* in being long, with a straight lower border. Dental formula: $I^3_3\ C^1_1\ P^4_4\ M^3_3$; incisors pointed, subequal in size, neither enlarged nor atrophied; canine tusks of moderate size, ovoid in section, definitely larger than incisors; premolars not molariform, but in Eocene stage of evolution; parastyles of P^1–M^3 relatively distinct cuspules; P^1 fairly primitive, with undivided amphicone, anteroposteriorly extended protoloph and lower antero-internal cingulum; P^{2-4} transversely elongated and having a V pattern, with thin metaconules confluent with crescentic protolophs, surrounded internally by cingula; M^1 squarish; M^2 largest of series; M^3 having ectoloph and metaloph virtually confluent, but forming a wide angle, about as in *Eotrigonias rhinocerinus*; trigonids of P_{2-4} the main functional parts, talonids consisting of anteroposteriorly trending hypoconids; lower molar trigonid and talonid crescents of rhinocerotid pattern.

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[1] The generic name is derived from παππος, grandfather, plus *alpha,* primitive, without, plus *keras,* horn. The specific name refers to the essentially confluent ectoloph and metaloph of M^3.

DESCRIPTION: The type specimen (A.M.N.H. No. 26660) was found at the same level and locality as A.M.N.H. No. 26611, *Eudinoceras mongoliensis* (Osborn and Granger, 1932, p. 1, fig. 1), and A.M.N.H. No. 26620, *Gobiatherium mirificum* (Osborn and Granger, 1932, p. 4). This locality appears on the section shown on pages 50–51 of the 1930 expedition field notes (Granger, MS). The specimen was found in the 28 feet of gray sandy clays disconformably underlying the Houldjin Formation, which are, in turn, conformably underlain by 80 feet of reddish and gray sandy clays with abundant *Lophialetes* and crocodiles at the bottom.

The type (figs. 1A, 1B, 2A, 2B) was evidently a mature individual, with much of the tooth pattern obliterated by wear. The skull has been considerably distorted by crushing and lacks the cranial region. The shape of the nasals and of the nasal incision is about like that of *Hyrachyus* and *Forstercooperia*, and not like that of *Hyracodon* or of later true rhinoceroses (even *Trigonias*) or amynodonts. The shape of the zygoma is intermediate between that of *Hyrachyus* and that of *Trigonias*. The lower jaw is long, with a straight lower edge, except for the symphyseal region, rather like that of *Trigonias*.

I^1 (figs. 1A, 2A) is represented only by alveoli, which are a shade smaller than the alveolus for the left I^2. I^{2-3}, right, are low pegs, somewhat elongated mesiodistally, with lateral flanges. C^1, right and left, are considerably larger than the incisors, with the tips much abraded; the relative size is more as in *Forstercooperia* than any other rhinocerotoid. The diastema is of moderate size. In P^1, the amphicone is not subdivided. The single internal loph, the protoloph, laps the postero-internal face of the amphicone. There is a complete external cingulum and an antero-internal cingulum. For P^2–M^3, as a whole, the closest resemblance is to *Eotrigonias rhinocerinus* Wood (1927). The parastyles of P^2–M^3 are somewhat more delimited from the paracones than are those of *Trigonias,* roughly like those of *Eotrigonias* and *Forstercooperia,* definitely less so than those of *Hyrachyus*. P^{2-4} are elongated along the transverse axis as are those of *Trigonias, Eotrigonias,* and *Forstercooperia,* as opposed to the more nearly equidimensional hyracodont premolars. These teeth are surrounded by continuous cingula, anteriorly, internally, and posteriorly; the external cingulum is continuous on P^2 but is interrupted by the paracone of P^{3-4}. At this stage of wear some characters have been obliterated, and the remains of the median valleys are isolated as small medifossettes. The protoloph was evidently the main transverse crest, swinging around posteriorly to, and joined by, the metaconule and including a hypocone region which becomes less distinct from P^2 to P^4.

The posterior crest is composed of the metaconule only, which was apparently much lower than the protoloph previous to wear. The total effect of the pattern is most nearly like that of *Eotrigonias*; there are suggestions of *Trigonias*, *Forstercooperia*, and *Hyrachyus*. The upper molars of the type specimen are strikingly like those of *Eotrigonias rhinocerinus*. They seem to have been nearly without cingula, except for the median valleys of M^{1-2} and the heavy posterior cingulum of M^3. The first upper molars are squarish teeth which were badly worn during life and severely damaged previous to collection, so that no pattern can be distinguished. M^2 is the largest of the series, has a typical primitive rhinoceros pattern, with the parastyle of about the *Eotrigonias* degree of isolation, which is less than that of *Hyrachyus*, but greater than that of *Trigonias*. M^3 is an interesting tooth. The ectoloph and metaloph are, at first glance, fully confluent; on closer examination, a slight change of trend is seen to mark their junction. There are also the remains of a posterior buttress, with an indentation lingual to it. The whole effect is closer to *Eotrigonias rhinocerinus* than to any other known form. Some third upper molars of *Trigonias* approach this pattern

The first lower incisors (figs. 1B, 2B), represented by their alveoli only, were somewhat smaller than the second lower incisors, which are a shade larger than I_3. I_{2-3}, less abraded than the upper incisors, are conical, expanded mesiodistally, and bounded by lateral flanges. C_1 is considerably larger than the incisors, somewhat expanded anteroposteriorly, like the incisors, with lateral flanges and abraded tip. The diastema is of moderate size. P_1 is composed mostly of a protoconid, with anterior, posterior, and postero-internal descending flanges and a complete cingulum, buccally and lingually. In P_2, the protoconid is still the main cusp, with anterior and postero-internal flanges, and a definite hypoconid blade; the cingulum is interrupted, so that there are antero-external, postero-external, antero-internal, and postero-internal cingula. The trigonid of P_3 is differentiated in rhinocerotoid fashion, with a large protoconid, from which the anterior crescent and a metaconid are fully delimited; the talonid carries a hypoconid as an anteroposterior blade. There are antero-external, postero-external, antero-internal, and postero-internal cingula. P_4 is a more advanced version of the same pattern, having a definitely rhinocerotid trigonid, a suggestion of a lingual flange on the hypoconid, and less prominent cingula. The trigonid and talonid crescents of M_{1-3}, like the trigonid of P_4, are fully rhinocerotid, differing from the more tapiroid dilophodonty of the Hyrachyidae. There is an antero-external cingulum on M_1 and definite external cingula in the valleys between the trigonid and talonid of M_{1-2}. Moderate posterior cingula can be distinguished on M_{1-3} and a moderate anterior cingulum on M_3.

A.M.N.H. No. 26667 (fig. 2C, 2D), a loose, nearly unworn, left upper premolar, supplies additional characters. This tooth, apparently P^2, from the ?Irdin Manha, possesses a protoloph that swings around posteriorly to the lingual end of the metaconule, which, however, abuts against it, thus damming the median valley. The gross effect of the transverse lophs is a V pattern, as in the worn third and fourth upper premolars of the type. The tooth was lost subsequent to the description and illustration.

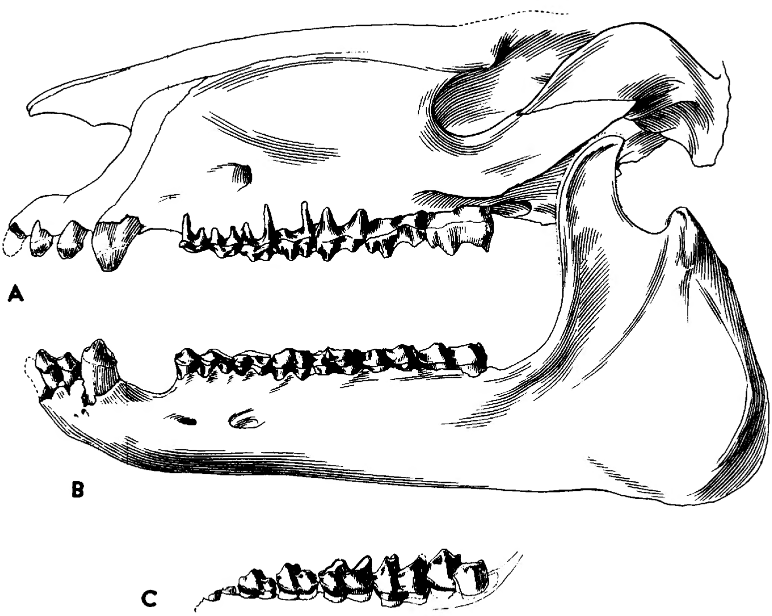

FIG. 1. *Pappaceras confluens*. A. A.M.N.H. No. 26660, left side of skull. B. A.M.N.H. No. 26660, labial view, left ramus of mandible. C. A.M.N.H. No. 26666, labial view, lower left cheek teeth. All × ¼.

Considerable additional information is furnished by a much younger individual, with only slightly worn teeth (figs. 1C, 2E), which appears to be referable to the same species (A.M.N.H. No. 26666, field no. 920), collected by Chih, 7 miles west of Camp Margetts, Inner Mongolia, September 16, 1930. The level is given as ?Irdin Manha beds (top). The close resemblance to the type lower jaw (A.M.N.H. No. 26660) tends to confirm the queried stratigraphic level. As compared with those of the type, the measurements of A.M.N.H. No. 26666 run slightly smaller, owing to two factors: first, the jaw belongs to a young adult individual, somewhat

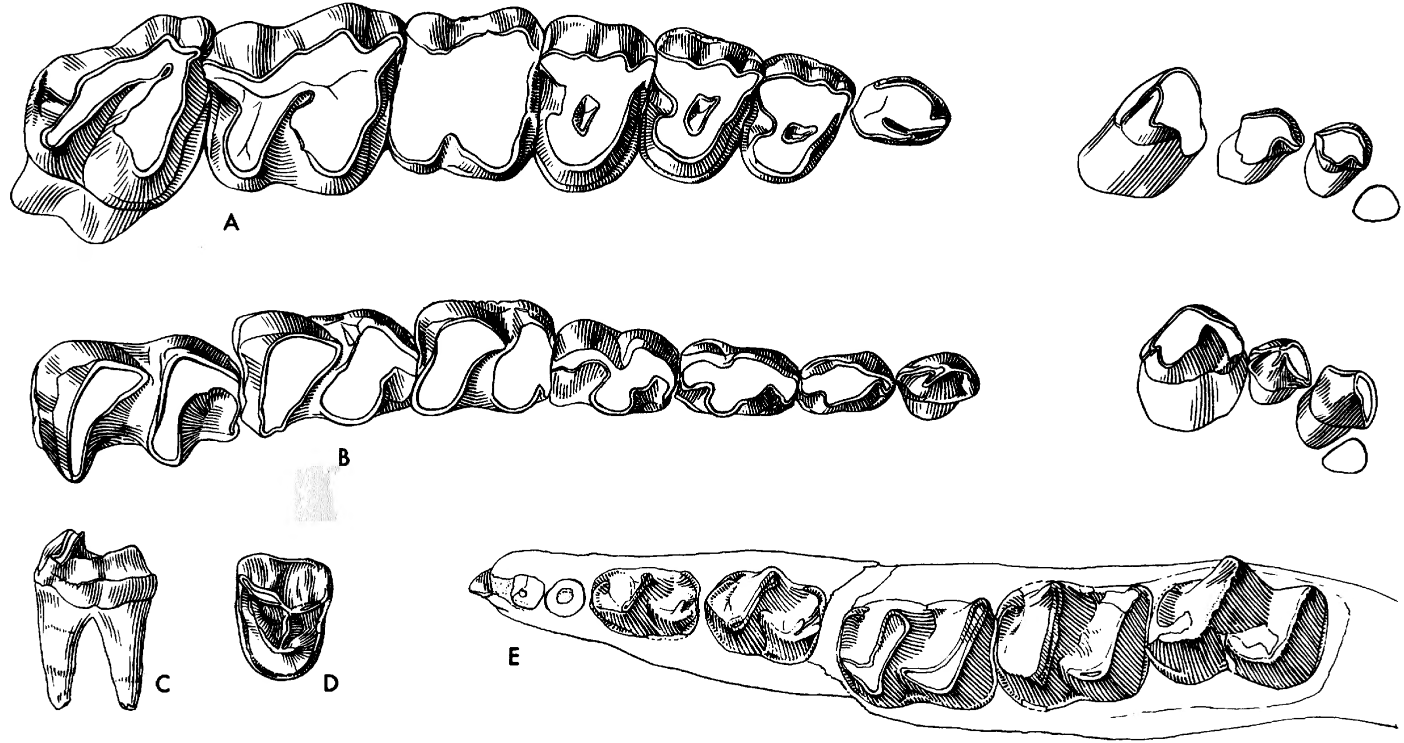

FIG. 2. *Pappaceras confluens*. A. A.M.N.H. No. 26660, right upper dentition, crown view. B. A.M.N.H. No. 26660, left lower dentition, crown view. C. P^2, A.M.N.H. No. 26667, mesial view. D. P^2, same specimen, crown view. E. A.M.N.H. No. 26666, left lower cheek teeth, crown view. All × ¾.

TABLE 1

MEASUREMENTS (IN MILLIMETERS) OF THE SKULL AND UPPER DENTITION OF *Pappaceras confluens* (A.M.N.H. No. 26660)

	Right	Left
Tip of nasal to anterior edge of orbit	—	210.5
Depth of nasal incision	53.7	50.5
Alveolus of I^1 to M^3	238.5	240.5
P^1–M^3	156.5	159.0
P^2–M^3	140.3	141.7
P^1–P^4	71.1	68.8
P^2–P^4	53.4	50.7
M^1–M^3	87.1	90.5
Alveolus of I^1, length	10.8	10.2
Alveolus of I^1, width	7.1	8.2
I^2, length	10.8	—
I^2, width	10.0	—
I^3, length	11.4	—
I^3, width	9.2	—
C^1, length	17.8	17.8
C^1, width	10.9	11.0
Diastema	25.8	22.4
P^1, length	17.9	17.6
P^1, width	11.2	11.4
P^2, length	15.9	15.9
P^2, width	21.3	21.4
P^3, length	17.1	17.2
P^3, width	26.4	26.4
P^4, length	19.7	18.5
P^4, width	29.1	30.2
M^1, length	24.8	26.6
M^1, width	30.1	29.1
M^2, length	31.4	31.7
M^2, width	31.9	32.5
M^3, length	31.9	31.7
M^3, width	35.2	34.7

short of its full growth, in which M_3 is still in process of eruption and P_{3-4} are barely worn; and, second, comparable tooth measurements indicate a slightly smaller individual. M_1 of A.M.N.H. No. 26666 was longer anteroposteriorly only because interstitial wear had not yet occurred. P_1 is represented by a portion of the alveolus; and P_2, by its two roots. P_3 and P_4 are functionally similar; the trigonids are crescentic in rhinocerotoid fashion; and the talonids carry, principally, hypoconids which are anteroposterior blades, which bite between the ectolophs and protolophs of P^{3-4} and against their metaconules. These hypoconids carry transverse

TABLE 2
MEASUREMENTS (IN MILLIMETERS) OF THE LOWER JAW OF
Pappaceras confluens

	A.M.N.H. No. 26660 Right	A.M.N.H. No. 26660 Left	A.M.N.H. No. 26666 Left
Symphysis to angle	—	376.0	—
Coronoid to angle	—	191.0	165.0
Symphysis to rear of M_3	—	229.5	—
P_1–M_3	157.5	159.0	—
P_2–M_3	142.5	145.0	139[a]
P_1–P_4	69.9	71.8	—
P_2–P_4	56.0	57.7	54[a]
M_1–M_3	88.1	89.1	83.9
Length of symphysis	89.3	89.3	—
Depth of ramus below P_2	50.0	54.3	—
Depth of ramus below M_2	56.7	60.8	54.7
I_2, length	—	11.9	—
I_2, width	—	9.6	—
I_3, length	—	11.4	—
I_3, width	—	8.4	—
C_1, length	16.9	16.9	—
C_1, width	11.4	11.2	—
Diastema	—	27.4	—
P_1, length	12.8	13.9	—
P_1, width	8.1	8.3	—
P_2, length	16.1	16.1	—
P_2, width	10.1	9.9	—
P_3, length	19.5	19.6	17.5
P_3, width	12.3	12.8	11.5
P_4, length	21.4	21.1	19.9
P_4, width	14.3	14.0	13.9
M_1, length	25.4	25.0	26.2
M_1, width	17.3	18.0	17.9
M_2, length	30.4	30.8	27.3
M_2, width	19.1	19.2	20.4[a]
M_3, length	34.1	35.5	30.9
M_3, width	19.6	19.7	19.6

[a] Estimated.

flanges on their lingual slopes, which are doubtfully, if at all, distinguishable in the type at its stage of wear. The trigonid of P_3 shows some delimitation into cusps, whereas in P_4 it forms a smooth crescent. The anterior cingulum of P_3 extends to both buccal and lingual slopes of the protoconid; in P_4, it covers about the same extent, from the buccal slope of the protoconid to the lingual slope of the metaconid region. The talonids of P_{3-4} are surrounded by continuous cingula on the three free sides. The trigonid and talonid crescents of the molars are definitely rhinocerotid, without any trace of the incipiently dilophodont hyrachyid condition. The anterior cingula lap around both buccally and lingually; the posterior cingula are limited to the posterior aspect only.

DISCUSSION

Although the preceding description and the figures establish *Pappaceras* as a very primitive rhinoceros, its exact systematic position is open to argument. It is not surprising that the various phyletic lines were less sharply differentiated in the Eocene than in the Oligocene. Any Eocene rhinocerotoid group could be arbitrarily extended to include one or more of the others. However, with regard to the families as they are now usually understood, the following distinctions are the most important. *Pappaceras* should be excluded from the Hyrachyidae, because it shows, in the lower molars, no trace of the incipient dilophodonty that parallels that of the tapirs. The full prominence of the premolars and the character of M^3 exclude it from the Amynodontidae. It differs from the Hyracodontidae in its unreduced canine, longer face, transversely elongated P^{2-4}, and rhinocerotoid M^3. Altogether, this genus seems to belong best in the Rhinocerotidae. To assign this genus to the Caenopinae would distort this subfamily to an inconvenient extent. Future evidence might make the Allaceropinae contain it logically. Provisionally, however, as a convenience, *Pappaceras* is assigned to the group Forstercooperiidae, Kretzoi's name for the diversifying true rhinoceroses of the Eocene (Kretzoi, 1940, p. 93) but reduced to subfamilial rank as the Forstercooperiinae, new term.

Beliajeva (1959), in a study of specimens taken from a coal mine near Vladivostok, described a new rhinoceros of late Eocene or early Oligocene age as *Eotrigonias borissiaki,* based on five teeth. These teeth were associated with *Procadurcodon carbonis* Gromova (1958) and *Rhinotitan orientalis* Janovskaya (1957). The lingual half of P^2 shows the protoloph and metaloph converging and connected by a high mure, a more advanced condition than in *Pappaceras* (fig. 2D). In P^4, the protoloph carries an incipient hypocone, and the metaloph is an isolated cuspule (the metaconule), around which the median valley escapes posteriorly. The distinction of the parastyle of M^1 is much as in *Pappaceras confluens.* The two teeth that Beliajeva interprets as P_3 and P_1 (1959, figs. 3, 4), when compared with those of *Pappaceras,* are more probably P_4 and P_2, respectively, because of their size and character. She gave their measurements as 19 by 15 mm. and 9 by 10 mm. "*Eotrigonias borissiaki*" is the same general size as *Pappaceras confluens,* but is slightly larger in most dimensions. P^2 has the protoloph and metaloph better separated, with a more advanced metaloph. P^4 has the hypocone incipiently demarked from the protocone and has a somewhat smaller metaconule, which is distinct from the protoloph, unlike the condition in *Pappaceras confluens.* The tooth interpreted as P_2 (the P_1 of Beliajeva, 1959, fig. 4) is somewhat more advanced than that tooth in *P. confluens* (fig. 2B), and the difference from P_1 is even greater. Altogether, Beliajeva's species is much better referred to *Pappaceras* than to *Eotrigonias.* On the other hand, specific status is clearly indicated by the geographic separation and somewhat more recent age, as well as the anatomical differences that appear in even the few teeth preserved. It should also be noted that, in Mongolia, *Rhinotitan* occurs, not in the Irdin Manha, but in the later Shara Murun.

With regard to Stock's tentative attribution of *Eotriogonias* to the Oligocene of California, the currently uncontradicted published record shows *Eotrigonias*(?) *mortivallis* Stock (1949) in the Titus Canyon Formation. As will be shown fully elsewhere (MS), *Eotrigonias*(?) *mortivallis* Stock (1949) is a composite form composed of hyracodont teeth and caenopine foot bones. The specific name *mortivallis* must go in the genus *Hyracodon,* whatever its validity as a species. The Titus Canyon Formation appears to be correctly considered as of early Oligocene age. "*Eotrigonias*" *mortivallis,* therefore, does not require further consideration in connection with Eocene true rhinoceroses.

The Forstercooperiinae, then, would include: *Forstercooperia* Wood (1939), replacing *Cooperia* Wood (1938), preoccupied; *Eotrigonias rhinocerinus* Wood and, provisionally, *E. petersoni* Wood; *Prohyracodon orientalis* Koch; *Pappaceras confluens,* new genus and species; and *Pappaceras borissiaki* (Beliajeva, 1959), new combination. It is still premature to say much about their exact ancestral relationships, although the suggestion (Wood, 1938, pp. 15–19) that *Forstercooperia* foreshadows the baluchitheres (Peraceratheriinae and other names) still seems likely. *Pappaceras* shows no special ancestral relationships. The idea of one ancestral Eocene true rhinoceros is obviously archaic, and the variety already known doubtless merely hints at future discoveries. However, *Pappaceras* is so much better documented than the Eocene forms hitherto described that it furnishes a much preferable point of departure for phyletic discussions. In a broad sense, it shows an Eocene true rhinoceros that could be ancestral to later forms.

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