

PALEONTOLOGYCONTRIBUTION TO THE PHYLOGENY OF *DICERORHINAE*

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The Betpakdala-beds (the Famine Steppe, Middle Asia), the age of which is not yet exactly known (on the border between Oligocene and Miocene?), have furnished among other materials a multitude of teeth of various rhinoceroses with practically no remains of skeleton. Among these a few small teeth may be distinguished, belonging undoubtedly to a representative of the genus *Dicerorhinus* (*Ceratorhinus*), apparently, to different specimens.

$P^1$ —left (135/91), crown complete (length—22, breadth—18, height—20 mm), of a triangular outline. Ectoloph massive (posterior portion), slightly inclined inwards of the crown, with parastyle well modelled, and proto- and metacone less pronounced. In lieu of protoloph on the border between protocone and parastyle there is a small crista not connected with the small conical deuterococone (see further); metaloph well developed terminating in a large conical tetartocone, linked by a thin bridge with a deuterococone of smaller size. Crochet marked by a fine indentation. Cingulum well developed on lingual side, but practically non-existent on labial side. Three roots are confluent, in the shape of two divergent plates, divided by a deep cavity on the labial side.

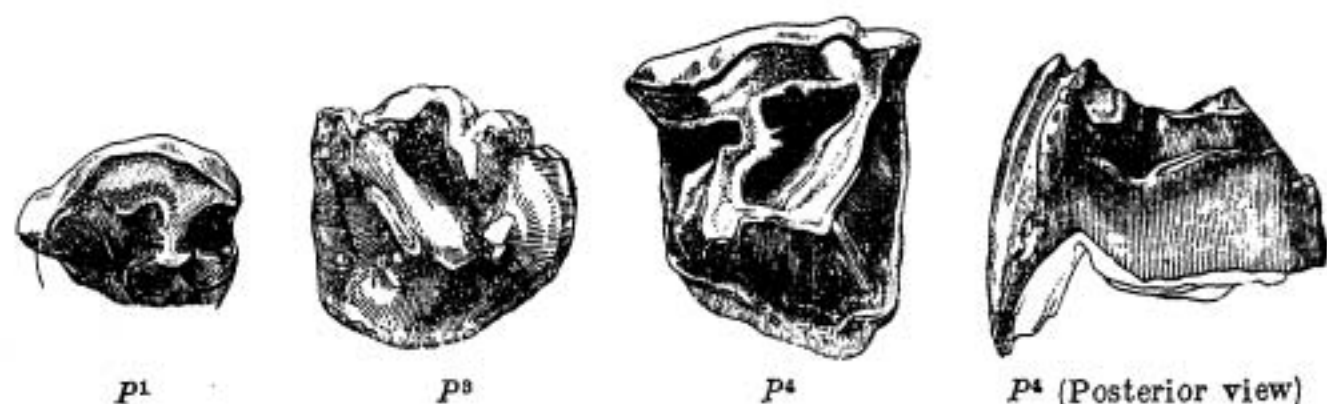
The nearest to the described  $P^1$  tooth stands the tooth mentioned by Roman [(<sup>1</sup>), p. 73, pl. VIII, Fig. 4] as belonging to *Rh. tagicus*. Another tooth of the same form (p. 71, pl. IX, Fig. 3), judging from the description, is distinguished by a more developed protoloph and deuterococone (?). The same tooth in *D. caucasicus* [(<sup>2</sup>), p. 381, Fig. 1] is of a similar character as the one described.

$P^3$ —left (135/96), crown incomplete (ectoloph broken off) with hardly any trace of wear. The preserved portion of the crown has a straight protoloph, terminating in a flatly-conical (compressed in the lingual-labial direction) deuterococone, stretched forwards and lingualwards; the ridge of the protoloph touched by abrasion (a narrow strip) in the lingual part, while it lowers in the labial direction; its position to the ectoloph remains unknown. The metaloph is in a worse state of preservation: of the labial end there is only the base retained, the crochet is missing (it might have been at the upper border of the metaloph?); the medial part is somewhat swollen; at the lingual end there is a robust tetartocone, conical, elongated labialwards almost to the mid-line of the crown. The metaloph adjoins the anterior end of the tetartocone. Between the tetarto- and deuterococone there is a narrow bridge not reaching the apex of the cones and having its own cuspule in the centre. The median valley broadens labially; the posterior one is

triangular. The cingulum is very strong on the anterior, lingual and posterior side; on the posterior side, at the tetartocone, it forms a thickened plate («hypostyle»).

Among the described  $P^2$  and  $P^3$  of *Rh. tagicus* there are none resembling the given tooth [(<sup>1</sup>), pl. VIII, Fig. 4, p. 73, Fig. 21 and others]; they are all more molariform, the transversal crests running parallel, without any bridge between them; a strong serrated crochet. The  $P^2$  of *D. caucasicus* [(<sup>2</sup>), p. 382, Fig. 1, and (<sup>5</sup>), p. 10, Fig. 1, Table 1, Fig. 1] have the following tendencies in common: the contour of the deuterocone, the presence of a bridge, the contact of metaloph with the anterior part of the tetartocone, protoloph not reaching ectoloph, metaloph tapering towards the ends, the presence of «hypostyle». However, the tetartocone is more approximated to the deuterocone, and the bridge is stronger—these are differences which may be due to the greater degree of abrasion of the crown.

$P^4$ —right (135/92), crown complete, moderately worn (length—26, breadth—32, height—26 mm), of a trapezoidal outline, with the antero-lin-



gual angle strongly protuberant lingualwards. Ectoloph not inclined inwards of the crown, straight, labial side almost flat, showing incipient undulation, with parastyle presenting a small stepped edge and a weak metastyle. Protoloph straight, narrow at the joint with ectoloph, somewhat swollen in the middle (protoconule) and on the lingual end, where it forms quite a robust deuterocone, flatly conical (flattened in the labial-lingual direction) inclining inwards of the crown; the anterior end of the deuterocone is swollen and projected lingualwards (see above); the posterior one, which is narrower, continues in the shape of a narrow bridge, uniting to the metaloph. Metaloph curved and narrower in the labial part; further it straightens, broadens, running almost parallel to protoloph (their lingual ends are slightly convergent); crochet consisting of three thin folds; tetartocone massive, conical, less flattened than deuterocone, not inclined inwards of the crown. The median valley is trapezoidal, with a minute fold crista; the posterior valley is triangular, broadly opening backwards. Cingulum strongly developed on the anterior, lingual and posterior side, lacking on the labial side. On the posterior side, at the tetartocone it forms a thick plate («hypostyle»). There are no roots retained.

Both by the character of the crown and the size, most closely related to the one described is  $P^4$  [(<sup>1</sup>), p. 73, Fig. 21] of *Rh. tagicus* from the lowest limestone beds of Orleans Selles-sur-Cher, a part of which belong to the Miocene; however, it is more stretched longitudinally, without any bridge between crests, with cingulum less developed. The tooth of *Rh. tagicus* mut. *ligericus* [(<sup>3</sup>), p. 113] is somewhat larger. The tooth of *Rh. tagicus* mut. *moguntiana* [(<sup>4</sup>), p. 16] bears still less resemblance—stretches still more longitudinally and has no anterior angle projected lingualwards, the bridge is also lacking (Oligocene-Chattien). The tooth

of *D. caucasicus* [(<sup>2</sup>), p. 383, Fig. 2, and (<sup>5</sup>), p. 12 and 14, Fig. 2 and Table 1, Fig. 2] is scarcely worn; the contour of the crown and the protoloph are of the same character.

*M*<sup>1</sup>—left (135/93) and right (135/88) belong to the same specimen; of the left there is a complete crown, of the right—a crown without the ectoloph, both marked by equally strong abrasion (length—35, breadth—35, height—16 mm). The crown is of trapezoidal outline (slightly narrowing backwards). The ectoloph is slightly sigmoid, its outer side slightly undulated. The ridge of the parastyle is sharp, stepped; the metastyle is well pronounced. Protoloph with a small modelled protocone and rather massive (at this stage of abrasion) antecrochet. Metaloph is shorter and less massive, with a small modelled hypocone, swollen in the middle part (fills out the posterior valley); crochet has the shape of a small yet wide fold (at this stage of abrasion). The median valley is narrow, curved, broadly opening lingualwards with a bifurcate apex, modelling a wide though not large crista. The posterior valley is sulciform. Cingulum is weakly developed, forms a cuspule at the entrance into the medial valley and a strong plate of «hypostyle» on the posterior side. The number of roots is unclear, the lingual ones fuse into one plate.



*M*<sup>1</sup>



*D*<sup>1</sup>

Among the rather varied material which is described under the name of *Rh. tagicus*, there are undoubtedly specimens closely approaching to the described tooth [e. g. (<sup>1</sup>), pl. VIII, Fig. 4; the same tooth: (<sup>4</sup>), p. 116, Fig. 41]—even with the «hypostyle» plate. The crown *M*<sup>1</sup> of *Rh. tagicus* mut. *ligericus* [(<sup>3</sup>), pl. II, Fig. 5] has an altogether different structure, with an enormous crochet and small antecrochet, a wide summit of the medial valley, the posterior one being triangular, open, etc. The tooth of *D. caucasicus* has no «hypostyle».

*M*<sup>2</sup>—left (135/89); crown without ectoloph, less worn than in *M*<sup>1</sup>; structure identical; owing to a lesser degree of abrasion, crochet is larger (reducing towards the base) and smaller than the antecrochet (broadening towards the base). Cingulum and «hypostyle» are of the same character. A good state of preservation show four lingual roots, two along the front wall and two along the hinder, each pair connected by a ridge, and besides both ridges are united by a longitudinal ridge into one common double-T-plate.

*D*<sup>1</sup>—right (135/87). There is a strongly worn crown of a milk molar (length—35, breadth—32, height—13 mm), probably pertaining to the same form. It is characterized by a very massive ectoloph, strongly inclined inwards of the crown, whereby the posterior part (tritocone) is distinguished by a stronger inclination than the anterior and is separated from it by a stepped edge. Protoloph very wide at this stage of abrasion with three enclosed valleys in the labial portion (complex outline of the unabraded); metaloph longer but less massive, with a small crochet. Cingulum strongly developed, independently bending about protoloph (entering into the medial valley).

The incompleteness of descriptions makes a comparison with milk teeth of *Rh. tagicus* impossible. The teeth shown in the figures [(<sup>1</sup>), p. 75, pl. IX,

Fig. 5, and p. 74, pl. IX, Fig. 1<sup>a</sup>] are to little abraded and are therefore difficult to compare; they are marked by a backward bend of the lingual end of the protoloph, which is not observed in the described tooth.

The lower jaw (135/40) with a set of teeth  $P_2-M_3$  might be referred to the same form.

There are no remains of the skeleton whatsoever.

The above description of the teeth of a small rhinoceros from Betpakdala gives convincing proof of their close relation to the teeth of *Rh. tagicus*. If one is to understand the species *Rh. tagicus* in as broad a sense as Roman does (<sup>1,4</sup>), one may assign them to that species, and profiting by the example of Roman himself, discriminate a particular variety *Rh. tagicus* var. *betpakdalensis*. This is all the more necessary, as so far we are in possession of too insignificant remains for the establishment of a new species. The most essential feature, by which this variety is distinguished from the typical *Rh. tagicus* from Portugal and from other varieties of Western Europe, is the weak molarisation of the premolars: the lingual ends of the transverse crests of the premolars of the betpakdalian form are connected by a bridge, and in  $P_3$ , besides, they run close to each other, and the metaloph is united to the anterior edge of the tetartocone. Another character of the new form presents the cingulum, forming in all teeth on the buccal side a «hypostyle» plate.

In determining the phylogenetic relations for *D. caucasicus* (<sup>2,5</sup>) which was considered as the middle Miocene stage in the development of the large-sized branch of *Dicerorhinae*, it was pointed out that it would be impossible to trace this branch to the *Rh. tagicus*, placed at the base of the small-sized branch, because the *Rh. tagicus*, as well as other representatives of the small-sized branch, have premolars well molarised (apart from other progressive vestiges). The peculiarities of the betpakdalian small rhinoceros indicated above—premolars faintly molariform and a «hypostyle» present, alongside of the flattened shape of the deuterocone, and protoloph not reaching ectoloph—just coincide with the main tendencies of the crown structure in *D. caucasicus*. Thus, the possibility is not excluded for the form described to be referred to the initial group of the branch *D. caucasicus*—*Rh. schleiermacheri*.

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