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Dentition and Classification

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Communicated by Prof. C.W. Drooger at the meeting of January 31, 1983

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ABSTRACT

Abundant remains of a new dichobunid artiodactyl, *Diacodexis pakistanensis* n.sp., have been identified in collections made at two localities in the Kuldana Formation of the North-West Frontier Province of Pakistan. This discovery, made by teams from Howard University and the University of Michigan, both working in collaboration with the Geological Survey of Pakistan, establishes the presence of *Diacodexis* on all the continents of the northern hemisphere at the beginning of the Eocene and possibly suggests an Asian origin for the Artiodactyla.

INTRODUCTION

Two teams of paleontologists have investigated the Mami Khel clay (Kuldana Formation), south of the village of Barbora Banda (spelled Barbara Banda on some maps), near Banda Daud Shah in the Kohat district of the North-West Frontier Province of Pakistan. The Kuldana Formation consists locally of the red Mami Khel clays, with lenses of sandstone and fine grit. The lithology of the lower part of the Kuldana Formation as exposed at Barbora Banda II has been described and discussed by Wells (in press). The mammalian remains were collected at two localities in these gritty lenses. The material recovered from Barbora Banda I in 1979 by the Howard University/Geological Survey of Pakistan was sent to Utrecht and prepared by H. Brinkerink. That collected from Barbora Banda II in 1980 by the University of Michigan/Geological Survey of Pakistan team was sent to Paris and prepared by D.E. Russell, Mme D. Sigogneau-Russell and J.-L. Hartenberger. The rodents from the HGSP preparation debris have been described by de Bruijn *et al.*, 1982. The dental

morphology and systematic position of the artiodactyl are discussed here; further descriptive anatomical papers on this species will follow.

The HGSP collecting team consisted of M. Arif, H. de Bruijn, S.T. Hussain, N. Khan and J.J.M. Leinders; the GSP-UM team included A. Jah, D.E. Russell, N. Wells and J.-L. Hartenberger. The Barbora Banda I locality (locality number 300 in the HGSP system) was discovered about 7 km west of the village of Banda Daud Shah and about 1.5 km south of Barbora Banda village. Barbora Banda II is situated about 800 m south of Barbora Banda village (latitude 33°15'12" N; longitude 71°9'6" E) and is thought to be in the same deposit that yielded mammals at Barbora Banda I; the two localities are considered contemporaneous. Additional specimens of the new species were found in some other localities of the Kuldana Formation (see Appendix 1).

The composition of the Barbora Banda fauna is unusual and unbalanced. Of the relatively abundant material collected at both localities, most is referred to the artiodactyl discussed here. A few specimens of a tapiroid perissodactyl represent a second form; more of this animal is found at Barbora Banda I than at Barbora Banda II. A single large incisor and a partial molar of an unidentified mammal were recovered at Barbora Banda II, indicating the presence of at least a third taxon. A small number of rodent incisors were found at both localities. Preparation and sorting of the matrix from Barbora Banda II are not yet complete, but members of the "Cocomyidae" and Paramyidae have been identified at Barbora Banda I. The presence of reptiles in the fauna is attested by a few remains of crocodylians at Barbora Banda II.

As the grit bands are thought to be flood plain deposits, it can be hypothesized that a large number of the small artiodactyls, accompanied by a few other forms, were surprised by a local flash flood and drowned. Such a flood sweeping through a limited area might account for the lack of faunal diversity in the sediments.

The flora is known from seeds of *Celtis* sp. (Ulmaceae), cf. *Ajunginucilla* sp. (Labiatae) and *Chara* sp. (Charophyta), which were collected at Barbora Banda I. Search in the Barbora Banda II matrix for palynological matter was unsuccessful.

There is some uncertainty about the age of the Kuldana Formation. It is generally regarded as early to middle Eocene (Cheema, Raza and Ahmad *in* Shah, 1977) and is recognized to be diachronous from east to west, being older in the west. The Barbora Banda localities, situated on the west side of the Kohat basin and in the lower part of the formation, could therefore be attributed to the early Eocene. At present it is uncertain whether more refinements will be possible (late early Eocene is sometimes suggested).

As morphological diversity within the sample of dental remains of the Barbora Banda artiodactyl is quite large, the presence of more than one taxon might be expected, but there is evidence that a large part of the diversity is due to post mortem deformation. For example, an examination of GSP-UM 209 reveals that, although the teeth in the left maxillary appear normal, those on the right side are clearly deformed, being twisted with their lingual portion

pushed anteriorly with respect to the labial part. Providing other examples, the teeth in the maxillary GSP-UM 211 are striking because of their subquadrate appearance; those GSP-UM 188 are antero-posteriorly compressed, or more transversely elongated. The difference in their aspect would suggest the presence of two taxa. This impression is strengthened by a considerable difference in the shape of M3/. In GSP-UM 211 the labial border of M3/ is perpendicular to the transverse axis of the tooth, whereas in GSP-UM 188 this border is strongly oblique. In GSP-UM 209 the teeth bear a closer resemblance to those in GSP-UM 188 than to those in GSP-UM 211, but the M3/ has a labial border that is straight, not sloping. This is in obvious conflict with the two types of tooth form. In HGSP 300 5003 the molars are subquadrate, but the M3/ has a sloping labial border. The molars of HGSP 300 5009 are also subquadrate, while the degree of sloping is different in both M3/'s, but the slope also differs from that in HGSP 300 5003. HGSP 300 5011 displays the transversely elongated teeth of GSP-UM 188. The degree of labial sloping of the M3/, however, is considerably less in HGSP 300 5011 than in GSP-UM 188.

The slope of the labial border of M3/ is variably expressed in both types of teeth. In consequence, its value as a taxonomic character here is nil. Deformation of the teeth can be shown in the tooth rows of a single specimen (GSP-UM 209 or HGSP 3000 5009). A larger sampling would probably yield all intermediates between the subquadrate and elongated types. HGSP 300 5009 is somewhat intermediate between, for example, GSP-UM 209 (right side) and GSP-UM 211. Therefore the shape of the teeth cannot be used to distinguish two taxa within this sample.

If it is accepted that our material has undergone considerable post mortem deformation, coupled with a degree of variability that is difficult to evaluate, it is clear that but few specimens display the original morphology. Some of the specimens that show the least deformation seem to be, among the lower jaws, GSP-UM 213 and HGSP 300 5003, and among the upper dentitions, the right side of GSP-UM 320 and the left side of HGSP 300 5009.

It should be mentioned that there is also variation in the degree of labial slope on the M3/ of the North American species and a length/width diversity in the upper molars that is somewhat similar to that seen in our material. The extent to which post mortem deformation might be responsible for this has not yet been investigated.

SYSTEMATICS

Order Artiodactyla Owen, 1848
Family Dichobunidae Gill, 1872
Subfamily Diacodexinae Gazin, 1955
Genus *Diacodexis* Cope, 1882

Type species: *Diacodexis metsiacus* (Cope, 1882) [= *D. laticuneus* (Cope, 1882) = *D. brachystomus* (Cope, 1882)].

Referred species: *D. chacensis* (Cope, 1875), *D. secans* (Cope, 1881) [= *D.*

olseni Sinclair, 1914], *D. robustus* Sinclair, 1914 and *D. gazini* Godinot, 1978.

Age and Distribution: Early Eocene, Europe and North America.

Diacodexis pakistanensis n.sp.

Type specimen: HGSP 300 5003, a left maxillary with P3/-M3/ associated with a left mandible with P/4-M/3.

Referred specimens: see appendix 1.

Type locality: Barbora Banda I; about 7 km west of Banda Daud Shah village and about 1.5 km south of Barbora Banda village (Kohat district, North-West Frontier Province of Pakistan), latitude 33°15'2" N, longitude 71°8'20" E.

Stratigraphical and geographical range: Kuldana Formation, Kohat district, North-West Frontier Province of Pakistan; Early Eocene.

Diagnosis: A small mammal with relatively high and short premolars and canines that are small, but larger than the first premolars. Short diastemata occur anterior and posterior to the P1, and there is a slight and variable space between P2 and P3. The upper molars are triangular; the cusps are not inflated and there is no incipient hypocone development. The paracone and metacone are anteriorly and posteriorly crested and the conules have median crests to these cusps. The lower molars have a small paraconid, relatively narrow but well basined talonids and the small entoconid is relatively far from the metaconid. The M/3 has a narrow talonid and a large hypoconulid lobe that opens broadly into the talonid basin (there is no constriction between the hypoconulid and the talonid). There is no indentation in the basal contour between the hypoconulid and the entoconid and only a slight one between the hypoconulid and the hypoconid.

Etymology: *pakistanensis*, genitive form of Pakistan, country of its origin. The holotype and other material of this species will be permanently housed in the Museum of Natural History in Islamabad, Pakistan.

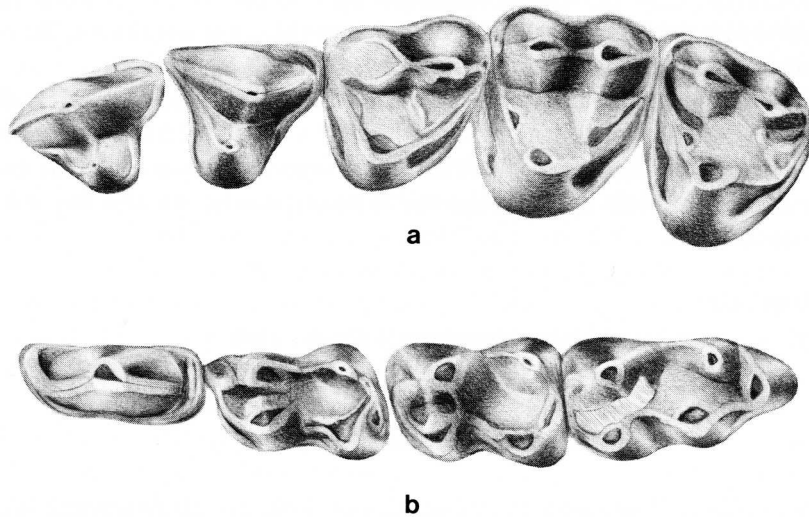


Fig. 1: *Diacodexis pakistanensis* n. sp., holotype, HGSP 300 5003 a. left maxillary with P3/-M3/; b. left mandible with P/4-M/3. Magnification 6x.

DESCRIPTION OF THE LOWER DENTITION

A complete dental formula of 3.1.4.3 is demonstrated by specimen HGSP 300 5016, in which all teeth or at least their roots are preserved. Small diastemata occur between all teeth from I/2 to P/2, and sometimes to P/3. Their size is variable but the largest is always situated between the canine and the first premolar.

In HGSP 300 5016 (the anterior part of which is figured in pl. 1, 1a) the incisors are not vertically implanted in the jaw: I/1 makes an angle of about 30° with the alveolar border, whereas the succeeding incisors become increasingly more vertical. I/1 and I/2 together form a single occlusal surface functionally. On I/2 the wear facet is at a right angle to the long axis of the tooth, whereas I/3 wears obliquely across the anterior part of the crown and I/1 obliquely across the posterior part.

I/1 is best preserved in HGSP 300 5246 (plate 1b shows the I/1 of specimen HGSP 300 5016). It is a simple, rather spatulate tooth, which bulges a little medially where it contacts the neighbouring I/1.

I/2 is well preserved on the left side of the skull and associated lower jaws of HGSP 300 5012 (the dentition of which is shown in pl. 1, 3a). The crown is wider and more symmetrical than that of I/1, with lateral borders diverging towards the apex. The tooth is orientated obliquely in the jaw.

On the same side of HGSP 300 5012, I/3 is also displayed (pl. 1, 3b). The root and crown of this tooth are orientated parallel to the tooth row, with the crown tilted anteriorly. It is implanted almost vertically in the jaw and the posterior crest of the tooth bulges out over the root. In slightly worn teeth the wear facet is perpendicular to the tooth axis, but as wear continues, the angle between the occlusal surface and the tooth axis decreases (see HGSP 300 5016 and 5010, pl. 1, 1 + 2).

The lower canine (pl. 1, 1a) is larger than I/3 and also P/1, but it is still a small tooth. The dorso-posterior and ventro-anterior borders of the crown are subparallel; wear occurs along the dorso-anterior crest (HGSP 300 5010), which is originally convex (HGSP 300 5014).

P/1 is a small single-rooted tooth (pl. 2, 5a + b), visible in HGSP 300 5010 and GSP-UM 322. It is notably shorter than the other premolars and the crown is simple with a steep anterior border and a longer, more sloping posterior crest. A small postero-lingual cingulum constitutes the principal difference that distinguishes P/1 from I/2, which are both small pointed teeth.

P/2 is well preserved in HGSP 300 5006 (pl. 2, 5a + b) and GSP-UM 322. Usually it has two roots, although these are sometimes fused to some degree (in HGSP 300 5005 the lingual side shows one root while the labial shows two). P/2 is appreciably longer than P/1 and is otherwise distinguished by the development of cingular shelves at the base and on each side of the anterior and posterior trenchant crests of the main cusp. Barely indicated antero-labially, the cingulum is wide and more or less basined antero-lingually and supports anteriorly a poorly defined protostylid. Postero-labially development varies from no shelf at all to a basining approximately equivalent to that in the antero-

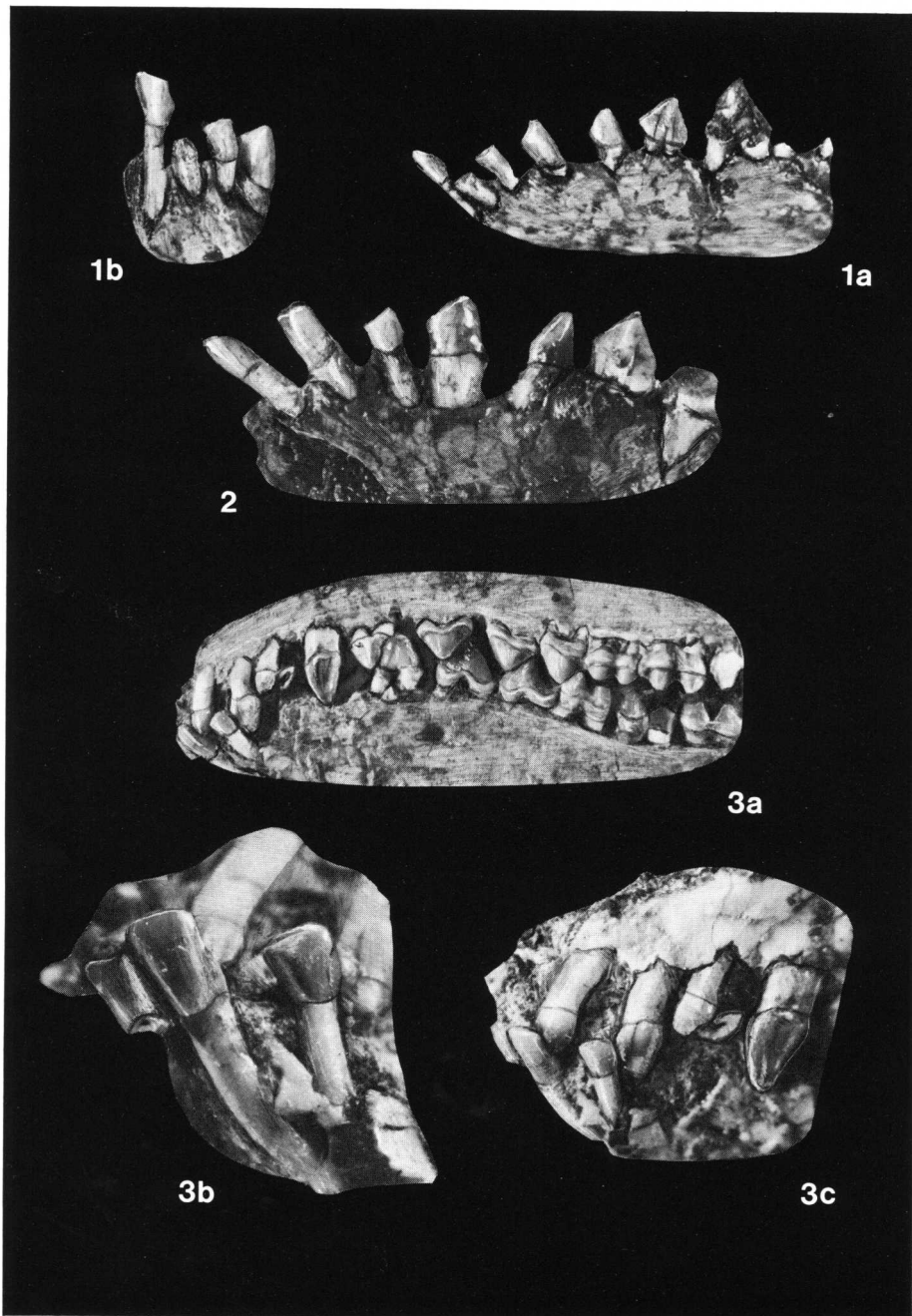


Plate 1: *Diacodexis pakistanensis* n.sp.

1. HGSP 300 5016; a. I/1-P/3, labial view, x4; b. I/1-C, anterior view, x6.
2. HGSP 300 5010; I/1-P/2, labial view, x5.
3. HGSP 300 5012; a. whole dentition, labial view, x3; b. I/1-I/3, antero-labial view, x11; c. I1/-C, I/1-I/3, labial view, x5.

All photographs were retouched.

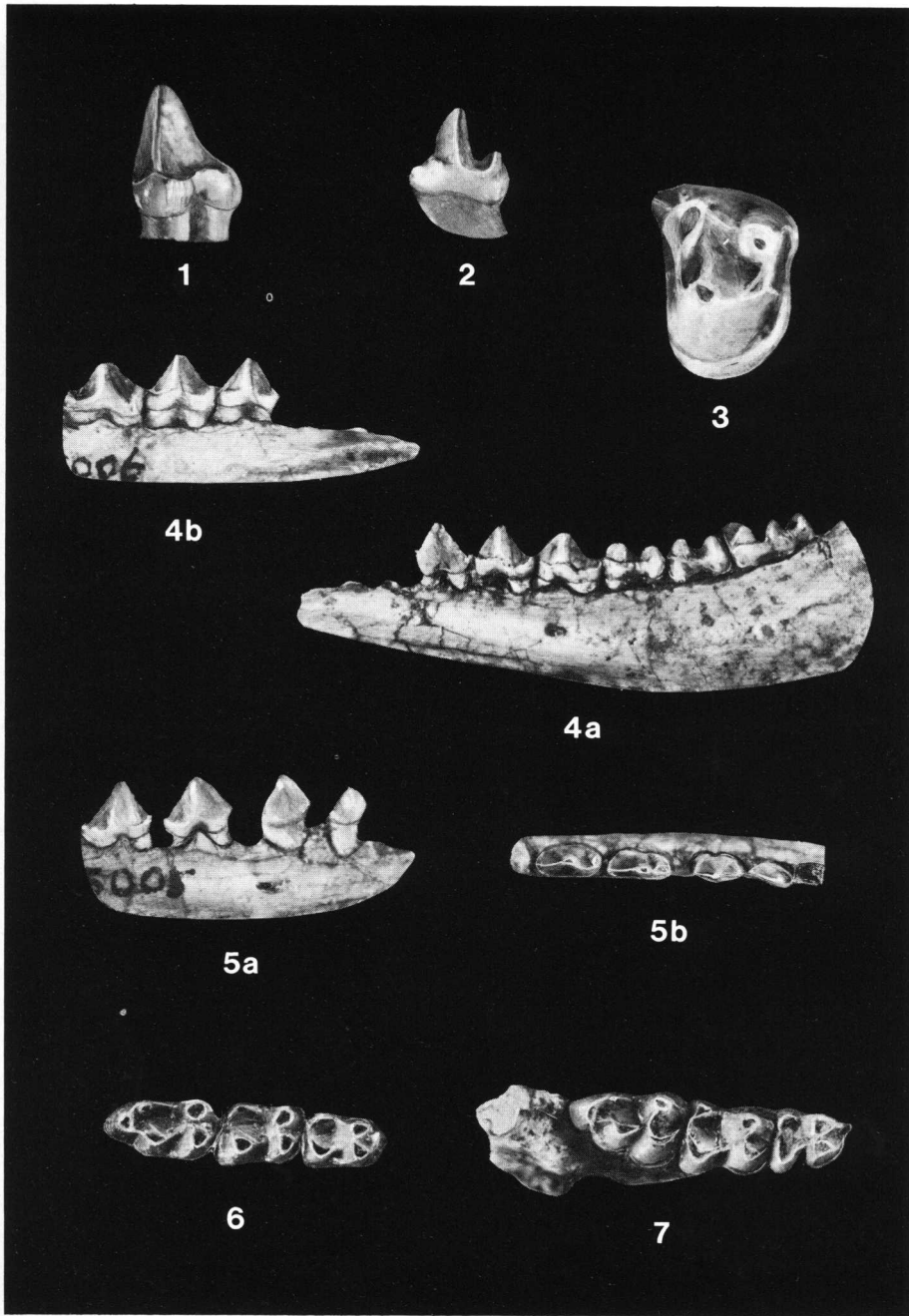


Plate 2: *Diacodexis pakistanensis* n.sp.

1. HGSP 300 5222; P3/, anterior view, x 7.5.
2. HGSP 300 5003, TYPE SPECIMEN; P3/, anterior view, x4.
3. HGSP 300 5213; trigonid, probably of M2/, x10.
4. HGSP 300 5006; a. P/2-M/3, labial view, x3; b. P/2-P/4, lingual view, x3.5.
5. HGSP 300 5005; a. P/1-P/4, labial view, x3.5; b. P/1-P/4, occlusal view, x3.
6. HGSP 300 5013; M/1-M/3, x4.
7. HGSP 300 5027; M/1-M/3, x3.5.

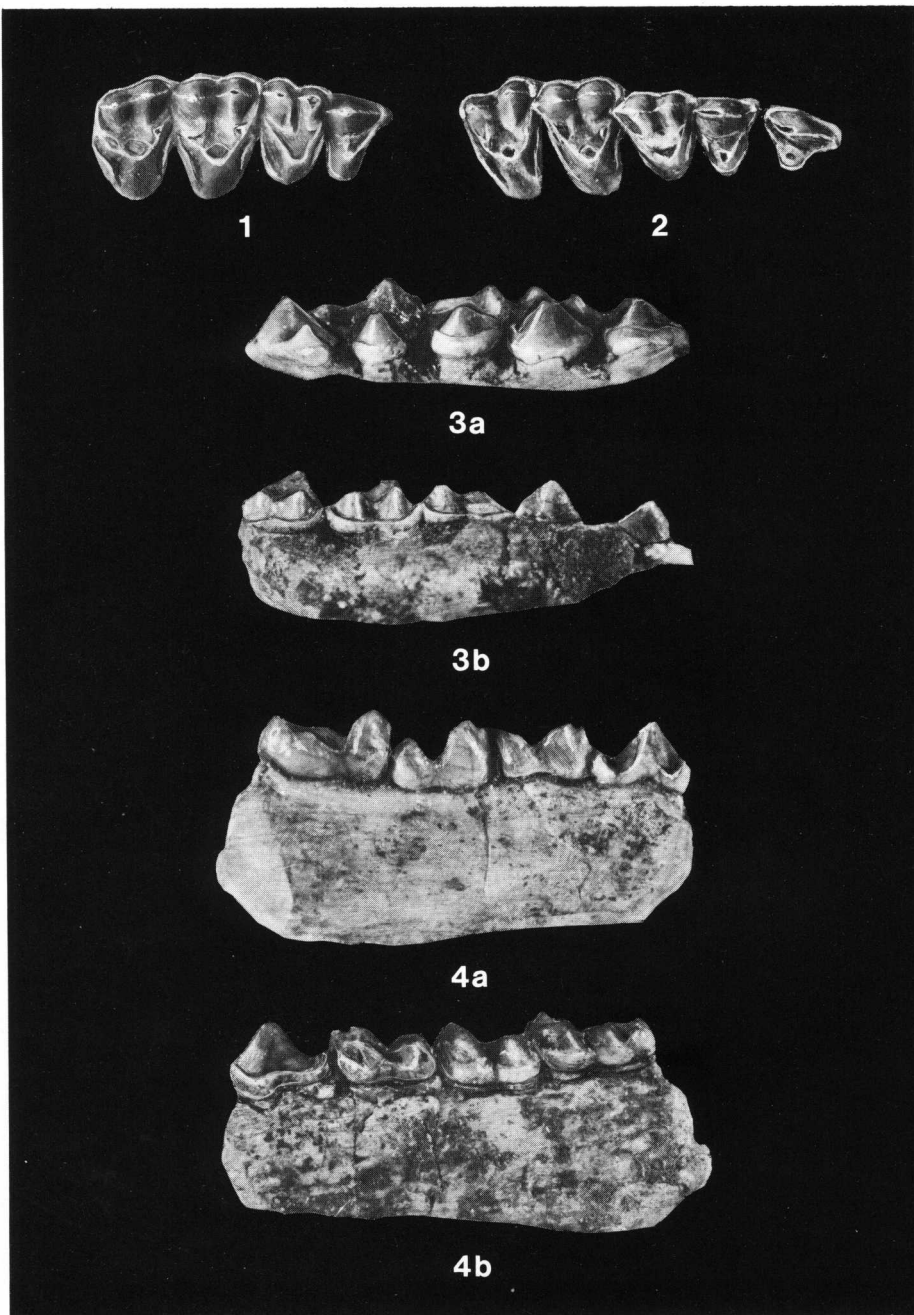


Plate 3: *Diacodexis pakistanensis* n.sp.

1. HGSP 300 5001; P4/-M3/, x4.
2. HGSP 300 5026; P3/-M3/, x4.
3. HGSP 300 5003 TYPE SPECIMEN; a. P3/-M3/, lingual view, x4; b. P3/-M3/, labial view, x4.
4. HGSP 300 5003 TYPE SPECIMEN; a. P/4-M/3, lingual view, x4; b. P/4-M/3, labial view, x4.

lingual position. Maximum expression is found postero-lingually, forming what could be termed a talonid. The posterior crest of the main cusp separates the two posterior basins and contacts the posterior extremity of the tooth at a small tubercle situated slightly lingually on the rim. A second tubercle sometimes occurs further lingually. The labial and lingual cingula are not continuous, but can be nearly so. This tooth varies considerably in length, width and development of the anterior and posterior lingual cingular basins. In GSP-UM 322 it is virtually identical to the P/3 of GSP-UM 213.

P/3 and P/4 are essentially more robust models of P/2. In P/3 (pl. 2, 4a + b) the anterior part of the crown is longer than that of P/2, forming a more symmetrical balance between the anterior and posterior halves of the tooth. The lingual and labial cingula tend to be continuous (for example, in HGSP 300 5006) and the cingular basins are wider (except on the antero-labial side, where no basining occurs). A more distinct protostylid is present at the antero-lingual corner of the antero-lingual basin.

P/4 (pl. 2, 4a + b) exaggerates the same tendencies (see, for example, HGSP 300 5006): the cingula become more pronounced, the basining accentuated, and the protostylid a distinct cusp.

The first lower molar (in, for example, the type specimen, fig. 1 b + pl. 3, 4) is of the typical tribosphenic type. It is longer than it is wide and the trigonid is moderately higher than the talonid. The trigonid bears a large cuspsate protoconid, a somewhat smaller metaconid, and a still smaller paraconid (although this cusp is always distinct) situated high on the metaconid. Cristids occur between the lingual cusps and the protoconid. The talonid bears a large hypoconid, from which a crista obliqua extends to the approximate middle of the trigonid, making contact with it slightly labial of the protoconid-metaconid notch. From this point a wear facet runs obliquely to the summit of the metaconid. The talonid basin is relatively narrow and deep, with its maximum depth occurring behind the level of the metaconid. A postcristid connects the hypoconid and the hypoconulid. The hypoconulid and entoconid are subequal in size and situated close to each other. As a result of this, the distance between the metaconid and the entoconid is large. Development of cingula is variable. Anteriorly the cingulum extends as far lingually as the base of the paraconid; labially it is weak or absent at the base of the hypoconid and the protoconid. Posteriorly it extends to the hypoconulid, which is situated on it. There is no lingual cingulum. As can be inferred from isolated molars, the number of roots is variable; sometimes there is one transversely elongated root below both the trigonid and the talonid, while sometimes one of these roots or both, is divided into two connate ones.

The second molar (fig. 1b and pl. 3, 4) is much like the M/1, but it is both somewhat longer and wider and its paraconid is smaller, though usually distinctly cuspsate. The anterior cingulum does not extend so far lingually as in M/1, and the crista obliqua usually stops when it reaches the trigonid, not being connected to the metaconid by a wear facet.

The M/3 has a large hypoconulid lobe, which makes it the longest of the

molars. Little or no constriction of the hypoconulid lobe occurs lingually, and the concavity that separates it from the hypoconid is only small. Hypoconid, hypoconulid and entoconid are not connected by any intermediate crests. An isolated M/3 (HGSP 300 5220) shows two fused roots under the trigonid and a single triangular one under the talonid.

DESCRIPTION OF THE UPPER DENTITION

The dental formula for the upper teeth is 3.1.4.3, as can be seen in the left maxillary of HGSP 300 5012 (pl. 1, 3a). The anterior two incisors are not implanted vertically in the jaw, but are much more vertical than the corresponding teeth in the lower jaw. Short diastema occur between all teeth back to P3/ in HGSP 300 5012, but in GSP-UM 198 and 211 P2/ and P3/ are in contact.

Neither of the I1/'s (pl. 1, 3c) is very well preserved in HGSP 300 5012. The root is curved and the crown was probably pointed, although it is worn. The anterior side is convex, the posterior side is flattened.

I2/ is in HGSP 300 5012 a compact tooth (pl. 1, 3c). It has very convex sides and a pointed tip and is slightly larger than the other upper incisors. Very few I2/'s are preserved.

I3/ (pl. 1.3c) is visible on both sides of HGSP 300 5012. It is a small single-rooted tooth with a convex anterior and posterior side and a pointed tip.

Both upper canines are preserved in HGSP 300 5012. They are relatively large and pointed and are nearly vertically implanted in the jaw (pl. 1, 3c). The main difference between the upper and the lower canine is the absolute crown length, larger in the upper canine; upper canines always lack anterior wear facets.

The only first premolars that are still in the jaw are in an occluded position (HGSP 300 5012, pl. 1, 3a), so that only the labial side is visible. Seen from this side, then, the paracone has a skewed triangular profile (the anterior side being shorter), the cingulum is interrupted at mid-tooth and two roots are present.

The second premolar (pl. 1, 3a) is preserved in GSP-UM 198, although it is damaged lingually. The paracone has subequal anterior and posterior trenchant crests. The cingula are continuous with a lingual cingulum that is broadened posteriorly.

P3/ in HGSP 300 5003 (fig. 1a, pl. 3, 3) is triangular in occlusal view but it is longer than it is wide. There is a large, symmetrical paracone; at its anterior and posterior base a small cuspule is formed on the cingulum; the cingula are continuous except lingually. The small protocone of variable form is connected to the paracone by a small ridge. Three roots are present.

P4/ (fig. 1a, pl. 3,3) tends to be more rectangular in basal contour than P3/ and the paracone tends to be more bulbous, although it preserves a trenchant aspect. The protocone is much larger than in the third premolar and there is a preprotocrista. In one specimen (HGSP 300 5011) a postprotocrista and a metaconule are present, but generally these are absent. The ridge connecting the protocone and paracone is often weak or absent.

The first molar of, for instance, the type specimen, is of the typical

tribosphenic kind (fig. 1a, pl. 3,3). It is almost as long as it is wide, with three main cusps. The paracone and the metacone are subequal in size and height and are vertical; the protocone is situated far from the lingual border of the tooth and its lingual face is strongly sloping and slightly convex. The conules are well developed and of about the same size, the paraconule being situated somewhat more labially. The metaconule is connected to the protocone by the postprotocrista and the paraconule is connected to the protocone by the preprotocrista; continuing the latter, with the same orientation, the preparaconule crista extends to the weakly developed parastyle. The postmetaconule crista completes the V-shaped trigon by its contact with the posterior cingulum at the postero-lingual base of the metacone. The metaconule is connected to the base of the metacone usually by a sharp, short ridge. A weaker ridge extends lingually from the base of the paracone, but only rarely does it reach the summit of the paraconule. A straight centrocrista is present, continued anteriorly and posteriorly along the same axis to the cingulum by the paracrista and metacrista. Usually no metastyle is formed at the junction of the metacrista and the posterior cingulum. Cingula are well developed and encircle the tooth, except lingually. A thickening forming a variable crestiform elevation occurs in the anterior cingulum, antero-labially with respect to the protocone; a similar thickening occurs in the posterior cingulum, posterior to the protocone, but it does not form a hypocone. The lingual part of the tooth is distinctly triangular, showing little or none of the antero-posterior broadening that characterizes the European and North American species.

The second molar is similar to the first (fig. 1a, pl. 3,3). It is usually a little more wide than it is long. As will be shown later on, absolute width is a good character for distinguishing between the two.

In general, the morphology of M3/ (fig. 1a, pl. 3,3) is the same as that of the preceding two, although the metacone is much smaller than the paracone and there is sometimes a metastyle. Also, the posterior cingulum does not extend as far lingually as it does in M1/ and M2/. M3/ is usually larger than M1/ and about the same size as M2/.

METHOD OF MEASURING

Most of the measurements were taken with the aid of a microscope with a mechanical stage and measuring dials; some were also taken by the same person with a graduated scale in the eyepiece of a microscope. All values were rounded off at 0.1 mm.

I/1 to P/1 and I1/ to P2/ were measured from the labial side; their length was measured as a maximum length, parallel to the base of the tooth crown (fig. 2a). With the canines the height was also measured, parallel to the posterior edge of the tooth in labial view (fig. 2b). P/2 to P/4 and P3/ and P4/ were measured in occlusal view; their length and width were measured as a maximum value parallel and perpendicular to the tooth axis (fig. 2c).

In the lower molars, total length, length of the trigonid (the posterior point being the deepest point of the endocristid), width of the trigonid, and width of

the talonid were measured. For all these parameters the maximum value was taken, parallel or at right angles to the tooth axis (fig. 2e).

As the tooth axis can be rather inexact and subjective, the line connecting the para- and metacone was chosen for reference in the upper molars. All parameters were measured parallel or perpendicular to this line. Along with maximum length and width, the distance between the tips of the para- and metacone was measured (fig. 2d; the distance between the labial cusps is abbreviated as "p-m"). As primitive mammals have triangular upper molars and advanced mammals have quadrangular ones, triangularity indicates primitiveness. If we then quantify triangularity, it might help to indicate the evolutionary stage of a species. This was done by putting the tooth in a quadrangle into which it just fitted and by measuring the areas anterior and posterior to the protocone, spaces not covered by the tooth (the hatched areas in figure 2d). The sum of these areas was then calculated as a ratio of the total area of the quadrangle in order to be able to compare teeth of different sizes.

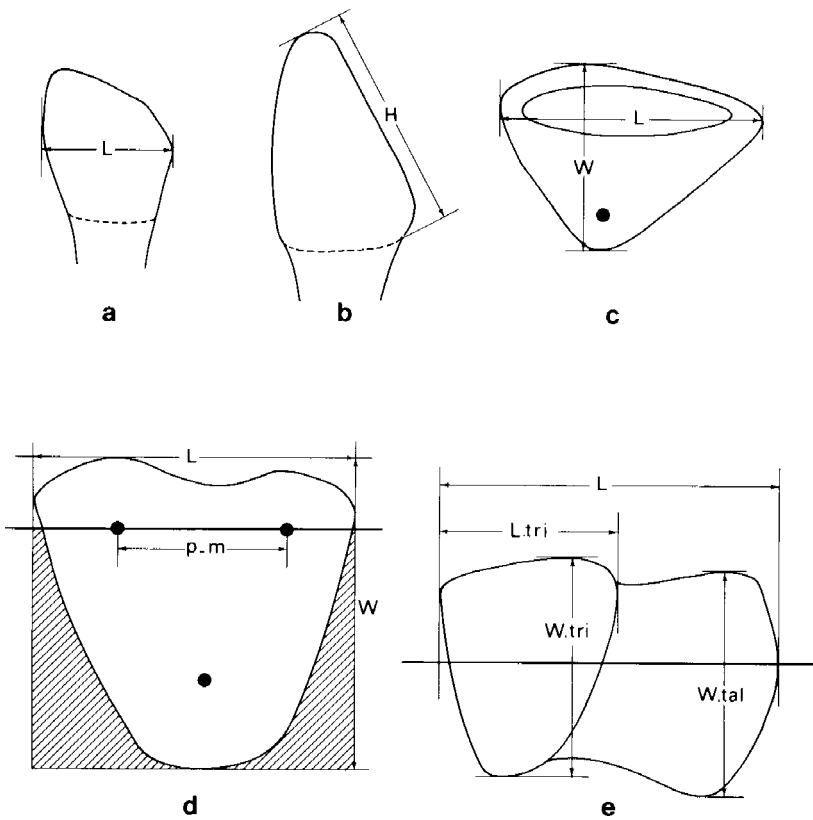


Fig. 2: Schemes indicating the method of measuring. a. Length of I/1-P/1 and I1/-P2/. b. Height of canines. c. Length and width of P/2-P/4 and P3/-P4/. d. Length (L), width (W), distance between para- and metacone (p-m) and area used for calculating trico (hatched) of the upper molars. e. Length (L), length of trigonid (Ltri), width of trigonid (Wtri) and width of talonid (Wtal) of the lower molars.

These values were obtained by drawing the teeth on paper with a millimetric scale, magnified 25 times, and by simply counting the number of squares. This parameter is called triangularity coefficient (trico).

Statistics were applied to a limited extent, solely to describe variation. Mean (\bar{x}), standard deviation (s.d.) and the coefficient of variance (CV.) were calculated. The definitions used are:

$$\bar{x} = \frac{x_i}{n}, \quad \text{s.d.} = \sqrt{\frac{(x_i - \bar{x})^2}{n-1}}, \quad \text{CV.} = \frac{\text{s.d.}}{\bar{x}} \cdot 100\%.$$

In the standard deviation n-1 was used instead of the usual n because we tried to extrapolate our measurements to the whole population of *Diacodexis pakistanensis*, while n only describes the measured sample. In cases where a parameter was not a linear one (i.e. trico and L/W) the mean and standard deviation used for calculating CV were calculated with x' instead of x ; $x' = \ln x$. In this way CV acts as a linear parameter. According to Simpson *et al.*, 1960, monospecific samples in mammals have CV values between 4 and 10 for linear characters. Gingerich, 1974, showed that this is sometimes higher, but we might accept Simpsons values as a standard.

VARIABILITY

In figure 3 a frequency distribution is given for the lengths of I/1 to P/1 and the height of the lower canine. As the number of teeth is rather small not much

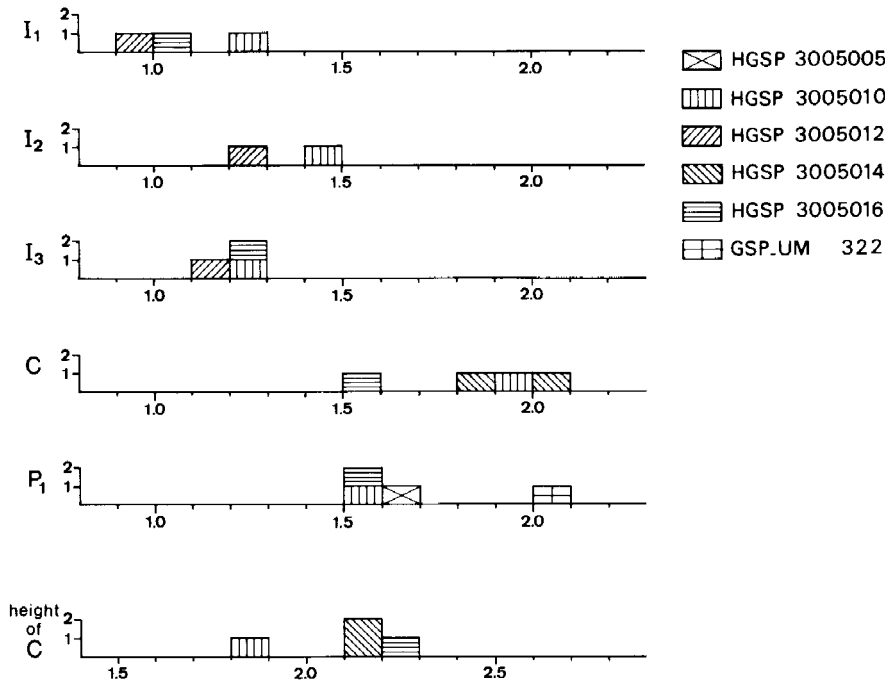


Fig. 3: Frequency distribution for the lengths of I/1-P/1 and the height of the lower canine (in mm).

can be said about the relative sizes, only that C and P/1 are probably larger than the more anterior teeth. The existence of a correlation between the sizes of teeth is also not clear, as the ratio of two teeth of one animal is often very different from the same ratio in another animal.

As already stated, many specimens seem to have undergone a considerable degree of post mortem deformation. This influences, of course, the measured values. There are now two sources of variation, i.e., variation between the living animals and differences in post mortem deformation. As this will only increase CV values, samples with CV values a little higher than 10 will still have to be considered as monospecific. Measurements and statistical data on P/2 to M/3 are summarized in Appendix 2. No CV value is, to our opinion, high enough to justify the division of the sample in two species.

The figures 4 to 7 present scatter diagrams concerning the lower cheek teeth: on the premolars, figure 4 (length and width); on the molars, figure 5 (length and width of trigonid); figure 6 (length and width of talonid), and figure 7 (length and length of trigonid). None gives the impression that two clearly separable groups are present.

Variation occurs also in some other characters that are not quantified. The development of the paraconid is one of them. In a tooth row it is always best developed in M/1, where it is usually a distinct cusp though considerably smaller than the metaconid (fig. 1). In the M/2 of the type specimen the paraconid is larger than the one in the M/3, while in HGSP 300 5013, for example, the paraconid is very small on the M/3 and absent in M/2 (pl. 2,6). In HGSP 300 5027 (pl. 2,7) it is ridge-like in the posterior molars, acting as a continuation of the paracristid that runs up the metaconid.

There is sometimes an angle in the paracristid (HGSP 300 5027, pl. 2,7) halfway between the proto- and paraconid. In some specimens (for example, HGSP 300 5213, pl. 2,3) a ridge runs from this angular part to the cingulum.

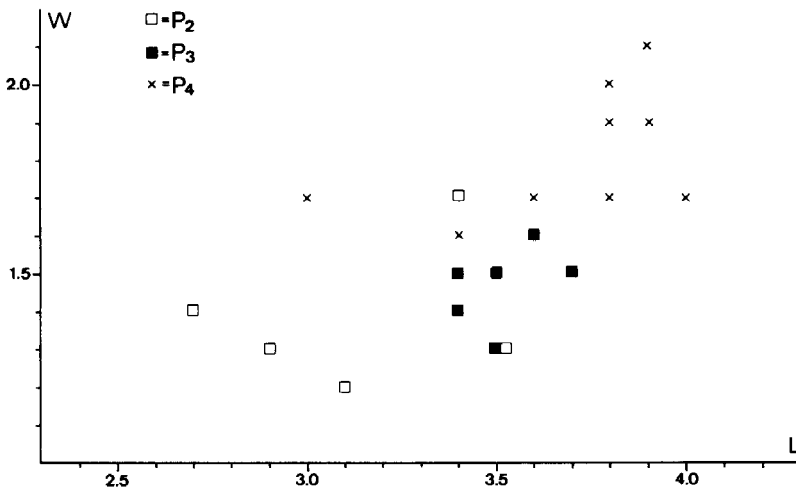


Fig. 4: Scatter diagram for length and width of P/2-P/4 (in mm).

There are also differences in the development of the crista obliqua. In HGSP 300 5029 it appears to run up the trigonid towards the metaconid in M/1, while in the other molars it ends at the base of the trigonid (this configuration is frequent in other groups also). In HGSP 300 5003 it runs a little way up the metaconid, but not as far as on M/1.

The cingulum is also developed to a variable degree. In the very worn HGSP 300 5005 it is absent, while in HGSP 300 5012 it is very strong.

In only one specimen was it possible to measure the sizes of the upper incisors and canine. In HGSP 300 5012 they are: I1/, 1.1 mm; I2/, 1.6 mm; I3/, 1.2 mm; C, 1.8 mm on the left side and 1.8 mm on the right side. The height of the left canine is 2.9 mm; the height of the right canine is 2.4 mm. P1/ was not measured as all specimens were damaged. P2/ was measured in only one case: its length in GSP-UM 328 is 3.3 mm and its width 2. mm. Measurements on P3/ to M3/ are summarized in Appendix 2. CV values are never large enough to justify division in two species. The very low CV values in the L/W and trico are caused by the definition of these values. They are both coefficients in which one variable parameter is shared by another variable parameter. If a part of the variability in both characters is caused by the same factor (in this case size; larger animals with larger teeth tend to have wider teeth as well), this source

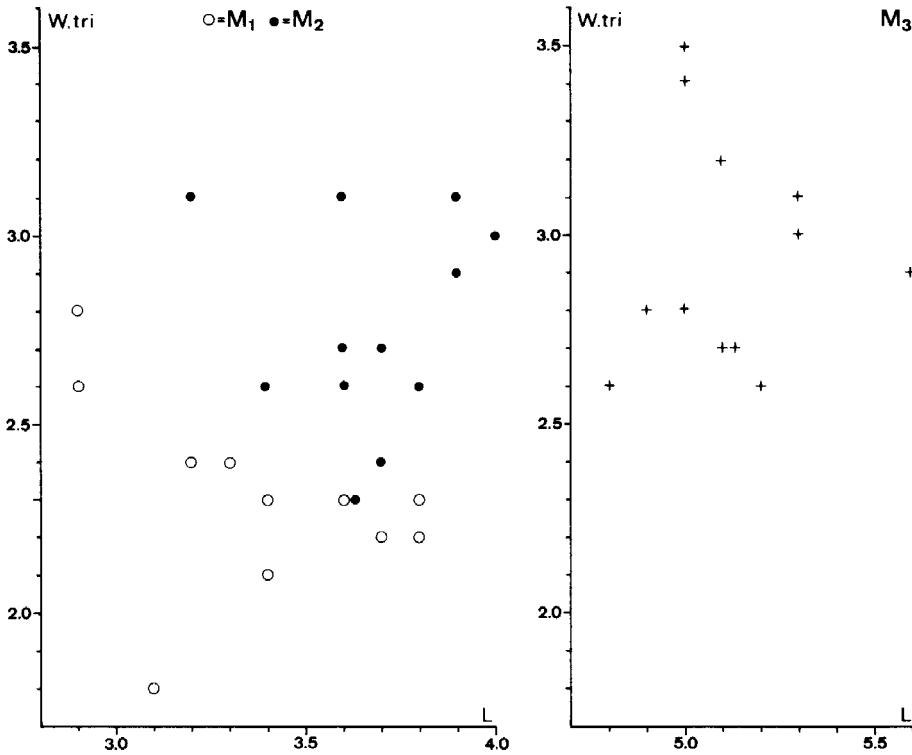


Fig. 5: Scatter diagram for length and width of trigonid of the lower molars (in mm).

of variability is neutralized when the two parameters are shared. The result is that only variation not caused by size remains.

A length-width scatter diagram for P3/ and P4/ is presented in figure 8 and the same diagram for the molars in figure 9. The last diagram gives the impression of the existence of two groups in both M1/ and M2/. These two groups, a form with wide and one with narrow molars, were already mentioned to indicate the presence of post mortem deformation. Besides that, the forms with the narrow first molars are not the same as those with the narrow second molars. This is not a good character upon which to divide the sample into two species.

Variation in not quantified characters occurs for instance in the form of the protocone lobe on the P3/. The cingula and other crests are very variable. Figure 10 presents sketches of the protocone lobe of P3/ to show this. The size of the protocone is also variable in this tooth. it is sometimes a real cusp giving rise to a distinct notch between it and the paracone, but this notch can be completely absent in a few other cases (the anterior views of P3/ in pl. 2, 1 + 2 show this). In P4/ the protocone lobe also shows variation. In HGSP 300 5026 it has a crescent shaped appearance, while in HGSP 300 5001 it is much more cusped because the cristae are barely developed (pl. 3, 1 + 2). The type specimen is intermediate. The P4/ of HGSP 300 5026 has a very narrow lingual cingulum, while HGSP 300 5001 has a broad one. In the former the cingulum is not inter-

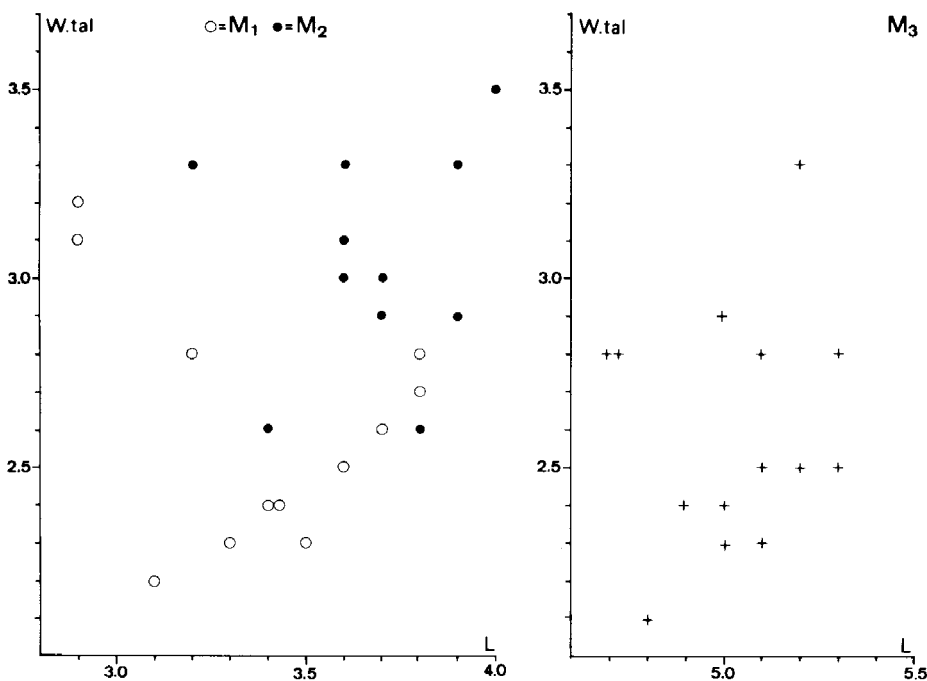


Fig. 6: Scatter diagram for length and width of talonid of the lower molars (in mm).

rupted lingually, but in HGSP 300 5003 it is. Most specimens lack a metaconule on P4/, but, for example, HGSP 300 5011 has a very distinct one.

In the molars variation exists in the size of the conules (very large in for instance HGSP 300 5066, very small in HGSP 300 5009), the place of the protocone with respect to the labial cone (anteriorly shifted in HGSP 300 5026, lying halfway between the para- and metacone in HGSP 300 5001) and other characters that are less conspicuous. Some of these are due to post mortem deformation.

COMPARISON

Material of the genus *Diacodexis* is abundant in the early Eocene of North America. As a whole, these species differ distinctly from *D. pakistanensis*: all American species are bigger; the lower molars have a more developed paraconid; the protoconid-metaconid notch is more open (deeper and wider); the crista obliqua contacts the posterior trigonid wall below the protoconid-metaconid notch (the contact in *D. pakistanensis* is more labial); the lower molars are wider and their talonid relatively shorter in the American species; the entoconid is higher and bigger, closer to the trigonid and therefore more distant from the hypoconulid, which is more medially located (on the M/1-M/2 of *D. pakistanensis*, the entoconid and the hypoconulid are small, subequal in size, and situated close together); on M/3, the more anterior position of the larger entoconid tends to produce a lingual bulge in the basal profile of the tooth and a concavity between the entoconid and the hypoconulid; there is also a concavity (of variable accentuation) between the hypoconid and the hypoconulid; these two concavities result in a greater isolation of the

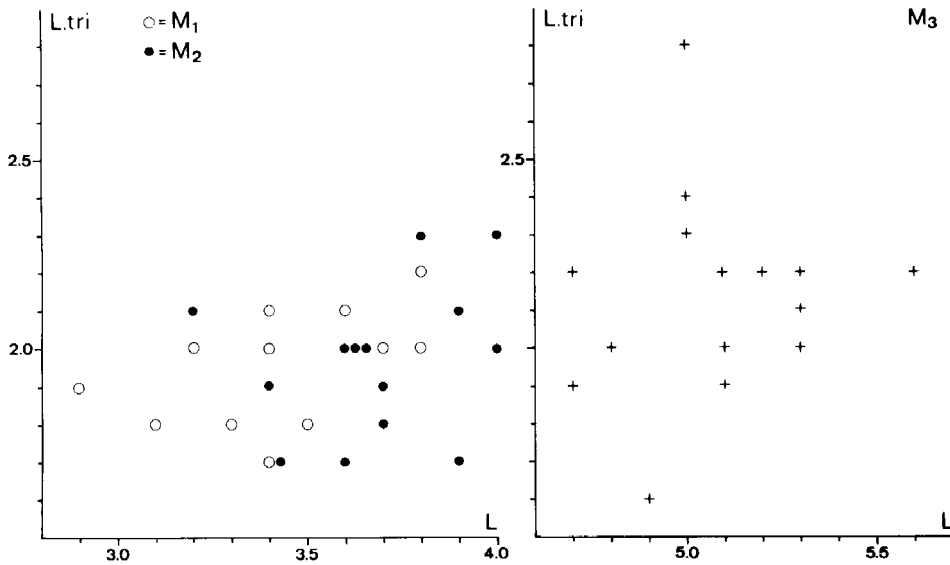


Fig. 7: Scatter diagram for length and length of trigonid of the lower molars (in mm).

hypoconulid lobe on the M/3 of the American species (in *D. pakistanensis* there is no lingual concavity and the labial one is usually shallower); the P/4 is more massive and wider, especially posteriorly; P/2 and P/3 are more slender, considerably longer and relatively lower teeth; M1/ and M2/ are less pointed lingually; anterior and posterior angulations in the basal contour of these teeth produce a greater antero-posterior diameter along the lingual border; a hypocone, though usually small, is occasionally present; P4/ is more transversely elongate; the crest between the protocone and the parastyle is weak or absent; P3/ is considerably longer. The sum of these distinctions, which are common to the four or five species of North American *Diacodexis*, indicates that they descended from a single stock that was not directly related to *D. pakistanensis*.

The early Eocene of Europe contains a variety of dichobunid artiodactyls, several of which represent species of *Diacodexis* (Sudre *et al.*, in preparation). The first of these to be described, *D. gazini* Godinot, 1978, is a small species known from a little material from the basal Eocene locality of Rians in southern France. The size and morphology of the known teeth (see Godinot, 1981) have contributed to the hypothesis that migration of at least part of the Wasatchian-Spannian fauna took place in an east to west direction. Like its closely similar North American relatives, *D. gazini* differs from *D. pakistanensis* in a greater lingual broadness of M1/ and M2/, along with a stronger development of the postero-lingual cingulum in these teeth. Its lower molar paraconid is larger, its

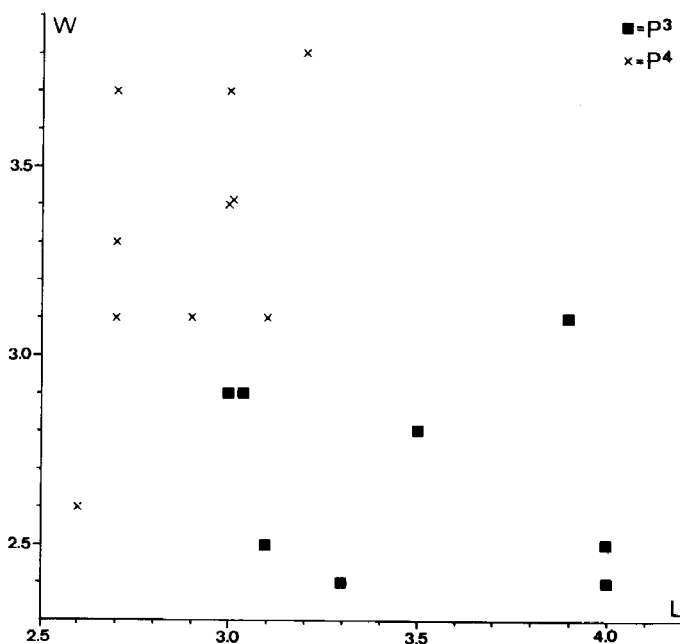


Fig. 8: Scatter diagram for length and width of P3/ and P4/ (in mm).

talonid shorter and wider than in the Pakistan form, and the M/3 hypoconulid lobe is accentuated by concavities on each side with a particularly pronounced step between it and the hypoconid. On the other hand, the crista obliqua contact with the posterior wall of the trigonid is more labial, as in the Pakistan form, and both are about the same size.

While *D. gazini* from Rians resembles the North American forms in most of its characters, samples from other localities, such as Dormaal (Belgium) and Condé-en-Brie (France), show different combinations of features that in some respects are closer to *D. pakistanensis*.

The M1/ or M2/ of the Dormaal species is slightly less broad lingually than in *D. gazini* from Rians, a trait that is found again in the undescribed Cuisian form from Condé-en-Brie. The M/3 talonid is narrow in the Dormaal form and the hypoconulid lobe opens widely into the talonid basin, contrasting with the wide talonid and isolated hypoconulid lobe in *D. gazini*. The entoconid, however, is located more anteriorly than in *D. pakistanensis* and contributes to the lingual bulge in the basal contour of the tooth that is also present in the North American forms.

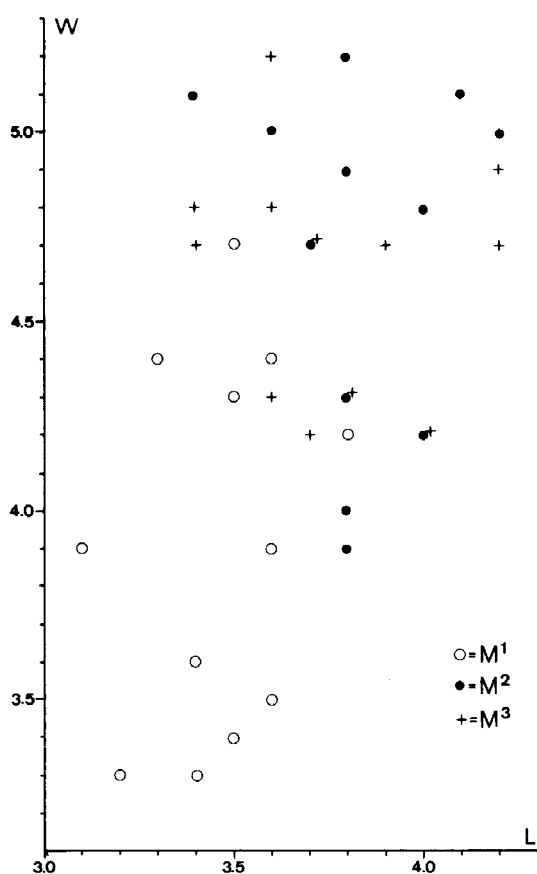


Fig. 9: Scatter diagram for length and width of M1/-M3/ (in mm).

— outline of tooth
 - - - crests
 ····· cingulum
 ○ position of protocone
 ▨ protocone lobe

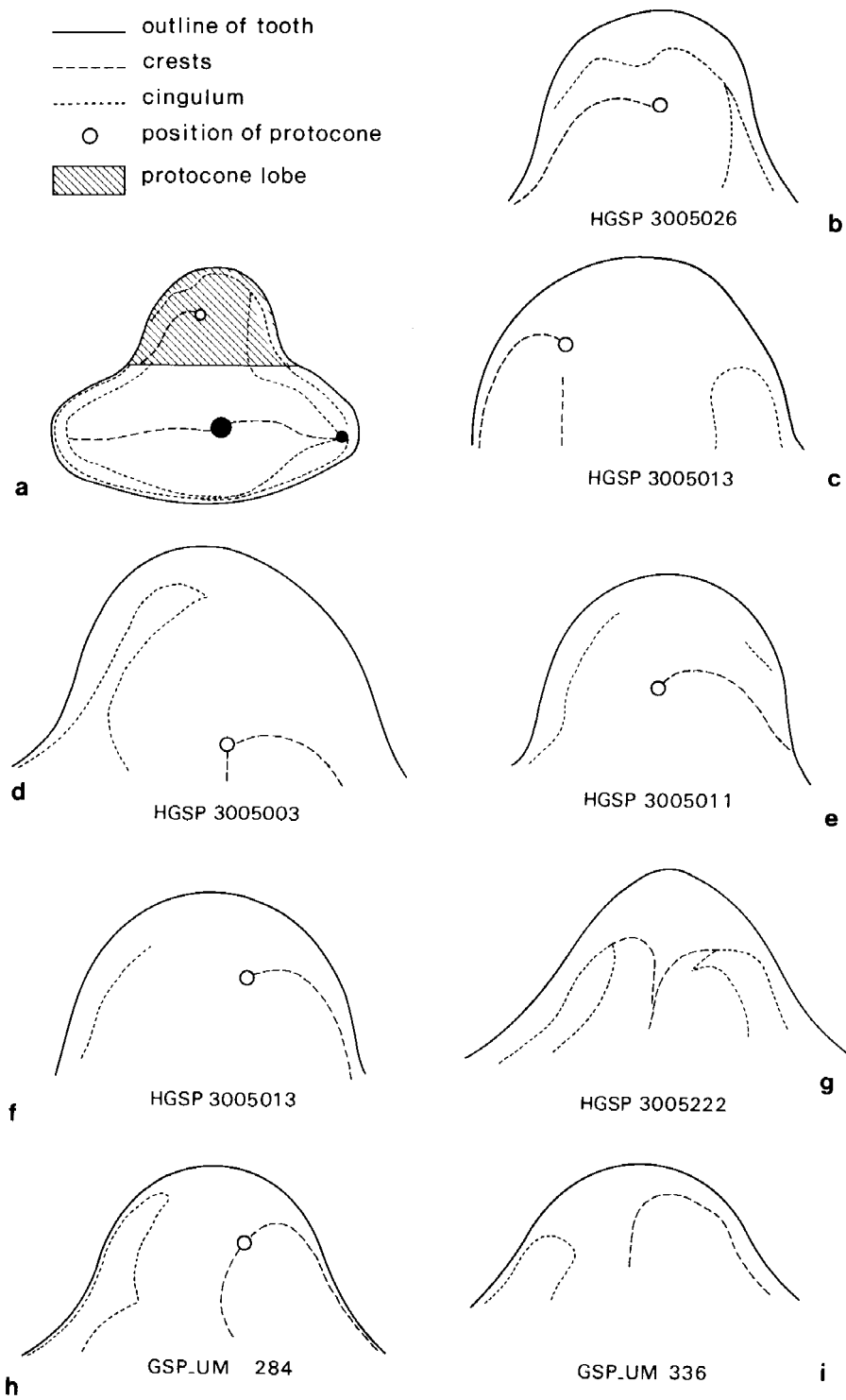


Fig. 10: Schematic representation of the protocone lobe of some P3/. a. Sketch of P3/, with hatched protocone lobe. b-i. Sketches of the protocone lobe in several specimens.

Another European form that is related to *Diacodexis* is *Messelobunodon*, from the middle Eocene locality of Messel (F.G.R.). The dentition of *M. schaeferi* Franzen, 1980 (in Franzen and Krumbiegel, 1980) is strongly reminiscent of that of the North American *Diacodexis* group. The small hypocone is also sometimes present in American specimens and the principal difference cited, the form of the P3/, can be regarded with some suspicion; only two individuals are known of *M. schaeferi* and our study has shown P3/ to be the most variable of the upper premolars. A younger species, *M. ceciliensis* Franzen and Krumbiegel, 1980, from Geiseltal (D.G.R.) shows that the genus is tending towards the *Dichobune* lineage and might be considered as transitional between the latter and *Diacodexis*. While *Messelobunodon* is probably a distinct genus (its anterior dentition is rather specialized and its skeleton is heavier and less cursorial than that of the North American *Diacodexis* (Franzen, 1981, Rose, 1982), it is nevertheless closely related to *Diacodexis*. With respect to *D. pakistanensis* most of its differing characters are those also seen in the American species.

Leaving the genus *Diacodexis* and turning to possibly related forms in Asia, *Chorlakkia* Gingerich *et al.*, 1979, from the opposite (eastern) part of the Kohat basin with respect to Barbora Banda, resembles the new taxon in size, but little material has so far been discovered; our knowledge of its variability is therefore severely restricted and comparisons, based essentially on the type specimen, are in consequence less valid than could be wished. Basically, the cusp pattern of the lower molars (the only teeth available) is similar to that in the Barbora Banda species, except for the absence of a paraconid in *Chorlakkia*; a small crescent-shaped cristid joins the protoconid and the metaconid, with no visible trace of an intervening paraconid. As the teeth in the type specimen are somewhat worn, it is possible that on M/1 a minute paraconid was present, but it is definitely absent in M/3. The talonid of the last molar is shorter and wider than that of *D. pakistanensis* and forms a more distinct basin; the hypoconulid of M/1 and M/2 in *Chorlakkia* projects more strongly. As in *D. pakistanensis*, however, and in contrast with the North American *Diacodexis*, the crista obliqua contacts the posterior wall of the trigonid labially with respect to the protoconid-metaconid notch.

The discovery of the morphologically primitive Barbora Banda species, which is certain to be an artiodactyl (as confirmed by the astragali that were found), makes it easier to include other Asian forms such as *Chorlakkia* and *Dulcidon* (see below) in the Dichobunidae. Both, in fact, can be regarded as more evolved forms of the same early artiodactyl stock that is represented in a more primitive state by *Diacodexis pakistanensis*.

After being placed in the mioclaenid Condylarthra by its discoverers, *Dulcidon gandaensis* (Dehm and Öettingen-Spielberg, 1958) was referred by Van Valen (1965) to the Paroxyclaenidae. Additional material and further analysis permits it now to be considered an artiodactyl, related to but distinguished from *Diacodexis* by its lower, more rounded cusps and crests, by less cingulum development, and by the lingual position of the paracone and

metacone. Only upper molars are referred to the species: the type, 1965-II-1 from Ganda Kas (Pakistan) and GSP-UM 106 and GSP-UM 274 from Chorlakkia (Pakistan).

The presence of still another small artiodactyl at Chorlakkia should be mentioned; it is exemplified by an undescribed well preserved M/3: GSP-UM 259. *Dulcidon* could represent the upper molars of a taxon whose lower teeth are as yet unknown, or the uppers of the undescribed form. It is even possible that the type lower jaw of *Chorlakkia* (for which no upper teeth have been identified) could be referred to *Dulcidon*, although this is not yet demonstrable.

Another Asian form, the enigmatic *Aksyiria oligostus* Gabunia, 1973, has been found in the early or middle Eocene Obayla Formation of the Zaisan Depression, Kazakhstan, S.S.R. Only a single upper molariform tooth is known; it is subquadrate, with an incipient hypocone and large conules (the metaconule is twinned), the anterior and posterior cingulum are well developed, but do not meet lingually. This tooth might be a dP4/. Sudre (1978, p. 45) cites it as resembling an unnamed middle Eocene French form. In any case, its evolutionary stage is above the level of *D. pakistanensis*.

Lantianius xiehuensis Chow, 1964, from the late Eocene of China, is probably an artiodactyl (Gingerich, 1976) despite the similarity of its upper molars to those of *Lushius qinlinensis* Chow, 1961, *Hoanghoniuss stehlini* Zdansky, 1930, and even the late Paleocene *Petrolemur brevirostre* Tong, 1979, all of which are also typified by a lingually continuous cingulum and a small or incipient hypocone, but are considered by some authors to be primates. *Lantianius*, however, would be rather remotely related to *Diacodexis*.

The other artiodactyls of Asia do not bear any significant resemblance to *Diacodexis* (see Coombs and Coombs, 1977a, b; Sahni *et al.*, 1981), or are too poorly known.

CONCLUSIONS

Diacodexis pakistanensis differs from the European and American members of the genus by either trends or details. It seems reasonable to consider the new species to be a distinctive member of the genus.

Concerning the anterior premolars, elongated in the American forms and virtually unknown in the European material, it is possible to derive the American morphology from one resembling that in *D. pakistanensis*. Other derived characters are apparent in the molars, like hypocone development and the lingual broadening of the M1/ and M2/. An increase in size with time has also been noted (Guthrie, 1967).

For these characters, *D. pakistanensis* would represent a more primitive stage in the evolution of the genus, but the reduction of the size of the paraconid and perhaps the entoconid indicate an opposite polarity.

However, there is a general morphological gradient from *D. pakistanensis* to the form from Dormaal, to the type material of *D. gazini* from Rians, to the relatively highly evolved, large sized North American species. This sequence, it should be emphasized, cannot be taken as a linear phylogenetic scheme; no

direct ancestor-descendant relationships are indicated, only a broad trend. In fact, it might be necessary to separate the Pakistani species into a different genus when the early Eurasian forms become better known.

D. pakistanensis is the most primitive species of the genus and thereby of the whole order; artiodactyls might, then, have originated in Asia. But if they have, it is probable that *D. pakistanensis* is not the ancestral form. Also, there is still uncertainty about the exact age of the Barbora Banda faunule. If it is late early Eocene, *D. pakistanensis* would be younger than the Wasatchian North American forms. In this case, it might be a relict form, prolonging to a certain degree the primitive state.

Diacodexinae were present on all the continents of the Northern Hemisphere in early Eocene times. Leaving aside the question of their place of origin, it is obvious that in order to reach or to leave Asia they had to cross either the Bering or the Turgai Straits. As the Pakistani form shares more characters with the European than with the American forms, it is reasonable to presume that the Turgai Straits presented the lesser barrier. This cannot yet be demonstrated for the Wasatchian-Spannian faunal elements that appear in Mongolia: *Hyracotherium*, *Hyopsodus* and *Coryphodon* for example. Further collecting, especially in Europe and Asia is necessary.

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APPENDIX 1

Material from Barbora Banda I used in this study:

- HGSP 300 5001 – P4/-M3/ left; P/4-M/3 left.
- HGSP 300 5003 – P3/-M3/ left; P/4-M/3 left.
- HGSP 300 5005 – P/1-M/3 right.
- HGSP 300 5006 – P/2-M/3 left.
- HGSP 300 5007 – M3/ right; M2/-M3/ left.
- HGSP 300 5009 – P4/-M3/ left; P3/-M3/ right.
- HGSP 300 5010 – I/1-P/2 right; I/2-C left; both upper canines, 2 upper incisors, one upper premolar.
- HGSP 300 5011 – P3/-M3/ left.
- HGSP 300 5012 – complete skull with lower jaws.
- HGSP 300 5013 – P3/-M3/ right and left; P/3-M/3 left; P/2-M/3 right.
- HGSP 300 5014 – I1/ left, C-M3/ left; C-M3/ right; I/1 left, C-M/3 left; I/1-I/2 right, C-M/3 right.
- HGSP 300 5015 – M/2-M/3 left.
- HGSP 300 5016 – I/1-M/1 left; M/2-M/3 left.
- HGSP 300 5017 – M/2-M/3 right.
- HGSP 300 5019 – P3/-M3/ left; P/4-M/3 left.
- HGSP 300 5025 – P3/-M1/ left; probably associated with a P2/.
- HGSP 300 5026 – P3/-M3/ right; probably associated with 5027.
- HGSP 300 5027 – P/3-M/3 right; probably associated with 5026.
- HGSP 300 5029 – M/1-M/3 left.
- HGSP 300 5131 – P3/, roots of P2/-M2/.
- HGSP 300 5147 – M1/-M3/.
- HGSP 300 5246 – I2/-I3/, left; I/1, I/3, C, right; I/1 left.

In addition to these, 59 isolated incisors, 11 isolated canines, 25 isolated premolars and 21 isolated molars were studied also.

Material from Barbora Banda II used in this study:

- GSP-UM 188 – P4/-M3/ left.
- GSP-UM 198 – P2/-M2/ left; P/2-M/3 left.
- GSP-UM 209 – P4/-M2/ left; P3/-M3/ right.
- GSP-UM 211 – P2/-M3/ left.
- GSP-UM 213 – P/2-M/3 right.
- GSP-UM 300 – P/2-M/3 right.
- GSP-UM 320 – P4/-M3/ right.
- GSP-UM 321 – partial M/1-M/2.
- GSP-UM 322 – P/1-M/3 right.
- GSP-UM 323 – P/4-M/3 left.
- GSP-UM 324 – M/1-M/3 right.
- GSP-UM 325 – P4/-M3/ left.
- GSP-UM 326 – M1/-M3/ left.
- GSP-UM 327 – P3/-M3/ right.
- GSP-UM 328 – P2/-P4/ right.
- GSP-UM 329 – M/2 in jaw fragment, left.
- GSP-UM 330 – M/3 in jaw fragment, left.
- GSP-UM 331 – P4/-M3/ right.
- GSP-UM 332 – M2/-M3/ right.
- GSP-UM 333 – P3/-M1/ left.
- GSP-UM 334 – M/2 in jaw fragment, left.
- GSP-UM 335 – P/4-M/3 right.
- GSP-UM 336 – P2/-M3/ left.
- GSP-UM 337 – P/4-M/3 right.

Additional material from Lammidhan (33° 38' 6" N; 72° 11' 35" E): GSP-UM 217 M2/ left.
Additional material from Chorlakki (33° 37' 17" N; 71° 55' 0" E): fieldno. 78184 M/3 right.
Additional material from Jatta Ismail Khel (33° 18' 29" N; 71° 18' 28" E): fieldno. 77089 partial
M2/-M3/ left.

APPENDIX 2

Measurements and statistical data on some cheek teeth (in mm, except in the case of "L/W" and "trico", in which there is no dimension). Symbols and method of measuring are explained in the text. "Width (of triginid)" means absolute width in the case of P3/ and P4/, and width of trigonid in the case of the molars.

number	length			width				L/W × 100			p-m		trico				
	P3/	P4/	M1/	M2/	M3/	P3/	P4/	M1/	M2/	M3/	M1/	M2/	M1/	M2/			
HGSP																	
300		3.0	3.2	4.0	4.1		3.7	4.5	5.2	4.8	71	77	91	1.5	1.7	162	191
5001		3.0	3.0	3.5	3.9	3.1	3.4	3.6	4.9	4.3	97	80	91	1.6	1.5		170
5003	3.9				3.2					5.0			63				
5007	3.0					2.9				3.8							
5009		3.0	3.1	3.7	3.6		3.4	3.4	4.0	4.3	91	92	84		1.4		
5011	4.0	2.7	3.3	3.7	3.6	2.4	3.7	3.4	4.1	4.4	97	90	80		1.4		101
5012	3.1	2.7	3.0	3.3	3.6	2.5	3.3	4.0	5.2	4.8	75	63	75	1.4	1.7	167	145
5013	3.9	3.3	2.7	3.6	3.6												
5013	3.9	3.3	3.7	4.1	3.5												
5013	3.9	2.7	3.4	3.7	3.8												
5025	3.0					2.9				3.8							
5026	3.3	2.9	3.4	3.6	3.3	2.4	3.1	3.7	4.8	4.8	89	75	69	1.6	1.6	222	238
5147			3.4	3.5	3.5			4.4	5.1	4.9	77	68	71		1.5		168
GSPUM																	
188				3.2				4.9					65				183
198	4.0	2.7	4.3			2.5	3.1							1.5			
209				3.3					5.3	4.9			67	1.3	1.6		
211		3.1	3.4	3.7	3.7	2.5	3.1	3.5	4.4	4.4	97	84	84	1.4	1.6	213	233
318		2.6	2.7	2.9				2.6						1.3	1.2		
320		3.4	3.6	4.0	4.2			3.5	3.9	4.2	92	95	85	1.5	1.9	201	235
325		3.2						3.8									
326			3.6					4.4			82			1.0		222	
328	3.5					2.8	3.3										
336	3.7	2.9															
n	11	14	15	14	14	9	12	12	13	15	12	12	13	10	13	6	8
\bar{x}	3.6	2.9	3.4	3.6	3.6	2.7	3.3	4.0	4.8	4.6	85	79	77	1.4	1.6	192	180
s.d.	.5	.3	.4	.4	.3	.3	.4	.3	.5	.5	10	11	10	.2	.2	.3	.5
CV	11.4	8.4	12.0	9.1	8.0	9.7	10.0	6.7	9.5	9.4	2.7	3.1	2.0	12.7	12.8	2.6	5.6

number	length			width (of trigonid)				width of tal			length of tri				
	P/2	P/3	P/4	M/1	M/2	M/3	P/2	P/3	P/4	M/1	M/2	M/3	M/1	M/2	M/3
HGSP															
300															
5001			4.0	3.4	3.6			1.7	2.3	2.7	2.4		2.1	2.0	
5003			3.9	3.7	3.7	5.0		1.9	2.2	2.7	2.6	3.0	2.0	1.9	2.3
5005			3.4	3.1	3.4	4.8		1.4	1.3	1.6	2.2	2.6	1.8	1.9	2.0
5006	3.4	3.5	3.8	3.6	3.6	5.1		1.7	1.3	2.0	2.5	3.1	2.1	2.0	2.2
5010	2.7						1.4								
5013		3.1	3.6												
5015					3.8	5.2				2.6	2.6	2.5		2.3	2.2
5027		3.5	3.9	3.3	3.9	5.0	1.5	2.1	2.4	3.1	2.3	3.3	1.8	2.1	2.4
5029				3.8	4.0	5.3			2.2	3.0	2.7	2.5	2.0	2.3	2.2
5030		3.4		3.4	3.6	5.1	1.4	1.7	2.1	2.6	2.4	3.0	2.0	1.7	1.9
GSPUM															
300						5.6				2.9					2.2
322	3.5	3.6	3.8	3.8	4.0	5.3	1.3	1.6	1.9	2.3	2.9	3.1	2.8	3.5	2.8
323			3.0	2.9	3.2	4.7		1.7	2.8	3.1	3.1	3.3	1.7	2.1	1.9
324					3.4	5.2							3.3		2.1
335			3.8	3.2		5.0		1.9	2.4		2.8	2.9	2.0		2.1
337				2.9	3.6	4.7			2.6	3.1	3.2	3.3	1.9	2.0	2.2
n	3	5	9	11	12	13	4	5	9	11	10	12	11	9	12
\bar{x}	3.2	3.4	3.7	3.4	3.7	5.1	1.5	1.4	1.8	2.3	2.8	3.0	2.6	3.1	2.6
s.d.	.5	.2	.4	.4	.3	.3	.2	.2	.2	.3	.3	.4	.4	.4	.4
CV	13.6	5.6	8.6	9.6	6.7	5.0	11.9	9.3	9.0	11.2	9.8	10.1	12.3	10.3	12.8
													7.5	8.7	9.9