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and a Review of *Schizotherium* Dentitions
(Perissodactyla, Chalicotheriidae)

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Additional *Schizotherium* Material from China, and a Review of *Schizotherium* Dentitions (Perissodactyla, Chalicotheriidae)

MARGERY CHALIFOUX COOMBS¹

ABSTRACT

Upper and lower cheek teeth of *Schizotherium*, collected from Urtyn Obo, East Mesa, Inner Mongolia Autonomous Region, Peoples' Republic of China, by the 1928 Central Asiatic Expedition of the American Museum of Natural History, may belong to *Schizotherium avitum* Matthew and Granger, 1923. Despite the fact that dental evidence is a poor taxonomic indicator for chalicotheres, teeth provide the only evidence available for comparing *Schizotherium* species. *Schizotherium avitum* is a relatively small (?) representative of *Schizotherium*, with long narrow M_3 , lower molar trigonid not wider than

talonid, narrow M_3 hypoconulid, and metastylid weaker than in *S. ordosium*, *S. priscum*, or *S. turgaicum* but stronger than in *S. chucuae*. *Schizotherium nabanensis* resembles *S. avitum* in many respects but is poorly known. Derived characters of the metastylid and M_3 hypoconulid suggest that *S. avitum* may be closest to *S. chucuae* among other *Schizotherium* species. Material described from China by Teilhard (1926) and Bohlin (1946) is of uncertain taxonomic position but is not referable to *S. avitum*.

INTRODUCTION

The primitive chalicotheriid genus *Schizotherium* is a relatively poorly known element of Oligocene faunas of Europe and Asia. Scattered material referred to six species (*S. priscum*, *S. turgaicum*, *S. avitum*, *S. chucuae*, *S. ordosium*, *S. nabanensis*) has been described from western Europe to China. *Schizotherium avitum* was designated by Matthew and Granger (1923) on the basis of an isolated M_3 from the lower Oligocene Ardyn Obo Formation of the Mongolian Peoples' Republic. Additional lower teeth (P_4 - M_3) from the Ardyn Obo

Formation were recently described by Dashzeveg (1974), and Hu (1959) referred two isolated teeth from China to *S. avitum*. Postcranials of this animal are unknown. The purpose of the present paper is to describe additional dental specimens of *Schizotherium*, possibly *S. avitum*, collected in 1928 from Urtyn Obo, Inner Mongolia Autonomous Region, Peoples' Republic of China. This material is compared with remains of other *Schizotherium* species in an attempt to improve understanding of the genus as a whole.

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ABBREVIATIONS

AMNH, Department of Vertebrate Paleontology, the American Museum of Natural History, New York
 LPGIN, Paleontological Laboratory of the Geological Institute of the Academy of Sciences of the Mongolian Peoples' Republic, Ulan Bator
 Mus. Hist. Nat. Lyon, Muséum d'Histoire Naturelle de Lyon, Lyon, France
 Mus. Natl. Hist. Nat., Muséum National d'Histoire Naturelle, Paris, France
 PIN, Paleontological Institute of the Academy of Sciences, Moscow, U.S.S.R.

CLASS MAMMALIA

ORDER PERISSODACTYLA

SUPERFAMILY CHALICOTHERIOIDEA GILL, 1872

FAMILY CHALICOTHERIIDAE GILL, 1872

SUBFAMILY SCHIZOTHERIINAE HOLLAND AND PETERSON, 1914

GENUS *SCHIZOTHERIUM* Gervais, 1876

Included Species. *Schizotherium priscum* Gervais, 1876, *S. turgaicum* Borissiak, 1920, *S. avitum* Matthew and Granger, 1923, *S. chucuae* Gabunia, 1951, *S. ordosium* Hu, 1959, *S. nabanensis* Zhang, 1976.

Revised Diagnosis. A small schizotheriine chalicotheriid; I_2^1 , C_2^1 , P_3^3 , M_3^3 ; molars less elongated than in other schizotheriines: upper molars almost quadrate, with ectoloph taller and less lingually slanted than in *Chalicotherium* but weaker than in other schizotheriines; crista but no crochet present on upper molars (see Butler, 1965, for definition); hypoconulid present on M_3 ; Mc (metacarpal) V present on forefoot; astragalus tall and narrow, articulating distally only with navicular; metatarsals longer and narrower (proportionally) than in any other chalicotheriid except *Borissiakia* (for example, see proportions for metatarsal IV of *S. priscum*; Coombs, 1974); no fusion of phalanges.

Discussion. The most recent broad rediscussion of *Schizotherium* was by Belyaeva (1954), with whose generic diagnosis many of the above points agree. A few of Belyaeva's diagnostic characters, however, are not given above and require further comment. According to Belyaeva, *Schizotherium* forefeet retain a trapezium; yet my analysis of published specimens suggests that while *S. priscum* did have a trapezium, *S. turgaicum* had strongly reduced or lost it, apparently independently and in parallel with *Moropus hollandi*, *Borissiakia*, and *Ancylotherium*. I find no evidence for Belyaeva's suggestion that Mc V of *Schizotherium* articulated with the unciform (hamate) rather than with Mc IV as in other chalicotheriids where Mc V is retained. My study of upper premolars of *Moropus* suggests that relative development of anterior and posterior transverse lophes (protoloph and metaloph) varies individually, partly as a result of wear. Comparison of relative development of these lophes in *Moropus*, *Phyllotillon*, or *Schizotherium* is therefore not especially useful.

Study of upper deciduous teeth of *S. priscum* and *S. turgaicum* (Coombs, 1976) suggested that dp^2 is more molarized in *Schizotherium* than in other schizotheriines in which this tooth is known. However, a characteristic chalicotheriid dp^2 (unmolarized) of *S. priscum*, figured with dp^{3-4} as "*Chalicotherium modicum*" by Stehlin (1905, fig. 63), suggests that the question of dp^2 structure in *Schizotherium* has not yet been fully resolved.

The diagnostic characters given above are in general primitive relative to character states in other Schizotheriinae. The small size, unelongated molars, and M_3 hypoconulid are found in no other schizotheriine genus. A fairly tall, narrow astragalus, long slender metatarsals, and unfused phalanges are also retained in *Borissiakia*, but *Borissiakia* differs in larger size, more elongated molars, absence of M_3 hypoconulid, and presence of a cuboid facet on the distal surface of the astragalus. Articulation between astragalus and cuboid in *Borissiakia* may be a primitive character, shared with such diverse perissodactyls as brontotherioids and rhinocerotoids, as well as with eomoropids like *Eomoropus* and the chalicotheriid *Chalicotherium*. However, the cuboid facet on the

astragalus of *Borissiakia* is much larger than that in *Eomoropus* and in this sense may be derived. *Borissiakia* is therefore derived in common with other schizotheriines in size and dental differences from *Schizotherium* but primitive or independently derived in having a large astragalus-cuboid contact. Among *Schizotherium* species, *S. turgaicum* is the only one for which an astragalus is known (Borissiak, 1921, 1946; Belyaeva, 1954), though Hu (1959) figured an astragalus referred to *Schizotherium* sp. from the Oligocene of Kansu. These specimens have no cuboid facet. So long as our knowledge of *Schizotherium* astragali remains so fragmentary and until our understanding of the primitive versus derived nature of the large astragalus-cuboid contact in *Borissiakia* is improved, exact phyletic relations between *Schizotherium* and *Borissiakia* will remain unclear. Additional derived characters, such as loss of Mc V, loss of crista and/or development of crochet, and strong increase in tooth crown height appear in various other schizotheriine genera (for example, *Moropus* and *Ancylotherium*) and further help to differentiate these forms from *Schizotherium*.

Radinsky (1964a) suggested that *Schizotherium* evolved from an *Eomoropus*-like form and cited the following characters differentiating *Schizotherium* from the eomoropids: emphasis of the ectoloph and the transverse lophs in producing shear on upper molars (involving, among other changes, strong development of the mesostyle and fusion of the parastyle with a crest from the anterior edge of the paracone), loss of first premolars, and development of clawed ungual phalanges with concomitant broad modifications in foot structure for dorsiflexion of the claws. *Schizotherium* can be considered derived in these characters in common with all other Chalicotheriidae. Chalicotheriids in general also differ from eomoropids in reduction of incisors and canines (see Coombs, In press), but development of anterior teeth in *Schizotherium* is unclear. Radinsky also noted the strong posterior migration of the protocone, more transverse (less anteriorly directed) orientation of the lingual part of the metalophid, reduction of the length of the premolar row, and loss of the M_3 hypoconulid as being characteristic of chalicotheriids; *Schizotherium* ap-

pears to be intermediate between eomoropids and other chalicotheriids in the development of these characters.

Teeth and postcranials together provide no difficulty for accepting *Schizotherium* as a primitive member of the Schizotheriinae very near the common ancestry of other members of the subfamily (with the possible exception of *Borissiakia*). Several authors (for example, Matthew, 1929, Coombs, 1974, 1976) have also suggested that *Schizotherium* is near the ancestry of the Chalicotheriinae. The latter notion is hard to document, however, for known *Schizotherium* postcranials show no indications of the pervasive derived characters seen in chalicotheriines. It is not difficult, therefore, to distinguish *Schizotherium* from such primitive chalicotheriines as *Chalicotherium pilgrimi* and *C. rusingense*, for whom postcranials have been described. *Schizotherium* teeth, because they are primitive in being low-crowned and quadrate, are more easily confused with teeth of chalicotheriines. However, even teeth suggest greater affinity between *Schizotherium* and other Schizotheriinae than with the Chalicotheriinae. Upper molars, especially M^3 , do show some trace of the ectoloph elongation between parastyle and mesostyle so pronounced in other schizotheriines. It is difficult to determine at this time where and how the Chalicotheriinae arose.

Schizotherium avitum Matthew and Granger

Schizotherium avitum Matthew and Granger, 1923, p. 4.

Schizotherium avitum: Matthew and Granger, 1925, p. 1.

?*Schizotherium* sp.: Matthew and Granger, 1925, p. 2.

Schizotherium avitum: Matthew, 1929, p. 519.

Schizotherium avitum: von Koenigswald, 1932, p. 22.

Schizotherium avitum: Colbert, 1934, p. 371; Colbert, 1935, p. 12.

Schizotherium sp.: Colbert, 1934, p. 373.

Schizotherium avitum: Belyaeva, 1954, p. 63.

Schizotherium avitum: Hu, 1959, p. 127.

Schizotherium avitum: Dashzeveg, 1974, p. 74.

Holotype. AMNH 19157, a right M_3 , collected in 1922 by the Central Asiatic Expedition of the American Museum of Natural History

from the Ardyn Obo Formation, "Promontory Bluff," at Erghilyin-Dzo, Dorono Gobi Province, Mongolian Peoples' Republic.

Hypodigm. LPGIN 21-(1), fragment of left mandibular ramus with P_4 - M_3 , collected in 1963 from the upper part of the Ardyn Obo Formation on the precipice of Bayan-tsav on the western part of the ridge Erghilyin-Dzo, Dorono Gobi Province, Mongolian Peoples' Republic; AMNH 20385, a fragment of an immature mandibular ramus with dp_4 and alveoli for M_1 , figured as ?*Schizotherium* species by Matthew and Granger (1925, fig. 3) and as *Schizotherium* sp. by Colbert (1934, fig. 10) and collected in 1923 from the Ardyn Obo Formation at Erghilyin-Dzo.

Revised Diagnosis. A *Schizotherium* species of smaller (?) average size than *S. priscum*, *S. turgaicum*, *S. chucuae*, *S. ordosium*, or *S. nabanensis*; trigonids and talonids of subequal width; length of M_3 more than twice exceeding its width; M_3 hypoconulid narrow and not so strongly developed as in *S. priscum* but stronger than in *S. chucuae*; metastylid more strongly separated from metaconid than in *S. chucuae* but less than in *S. priscum* or *S. turgaicum* or *S. ordosium*.

Schizotherium cf. *S. avitum* additional material: AMNH 26061, left maxilla with P^3 - M^3 and right maxilla with P^2 - M^3 , collected in 1928 from "Ulan Gochu" beds, Urtyn Obo, East Mesa, Shara Murun region, Inner Mongolia Autonomous Region, Peoples' Republic of China; AMNH 103336, a left mandibular ramus with P_4 - M_2 and alveoli for P_2 - P_3 , collected in 1928 from the ? "Baron Sog" beds at Urtyn Obo, East Mesa (see fig. 3). Hu (1959) referred isolated upper and lower molars from the Hota region of Inner Mongolia to *S. avitum*, but I consider reference of these incomplete specimens to be provisional.

Distribution and age: early Oligocene (Sannoisian) of central Asia.

Comments on Chinese and Mongolian *Schizotherium* localities: Figure 1 is a map of localities in Mongolia and China that have yielded fossils attributed by at least one author to *Schizotherium*. Dashzeveg (1974) recently discussed the Ardyn Obo Formation following concentrated studies in the area by Soviet and

Mongolian workers. He used the term Erghilyin-Dzo as appropriate for the large, 60-km. long badland from which the type of *S. avitum* came; the term Ergil-obo (Ardyn Obo) is restricted as a locality name to the southeast edge of this badland. Dashzeveg (1974) differentiated four bone-bearing strata at Erghilyin-Dzo. LPGIN 21-(1), referred to *S. avitum*, came from the upper beds (*Embolotherium* zone) of Dashzeveg, composed of light yellow, rather rough-grained spit-bedded, sandstones and a yellow-brown gravel. The type of *S. avitum* (AMNH 19157) was collected at Camp Ardyn Obo, situated near the large cairn where the Erghilyin-Dzo escarpment makes a near right-angle bend from east-west to north-south (Berkey and Morris, 1927, fig. 84). Dashzeveg (1974) noted that Berkey and Morris discussed the deposits at this locality as a single bone-bearing thickness, without differentiating the four fossiliferous zones later observed by Soviet and Mongolian workers.

However, study of the geologic section at Camp Ardyn Obo by Berkey and Morris (1927, fig. 86) suggests that the American geologists did have some conception of the different lithologies on the escarpment but that they found fossils only at one level, in the middle to upper part of the "Middle Member" (= Gray and Yellow Sands), below the "Yellow Sands and Gravels." A comparison of lithologies and faunas cited by Dashzeveg (1974) and Berkey and Morris (1927) suggests that the American collection, including the type of *S. avitum*, may have come from the river delta beds in which the Soviets and Mongolians "encountered perissodactyls (*Parabrontops gobiensis*, *Colodon inceptus*?), *Ardynia praecox*), artiodactyls (*Lophiomeryx gobiae*, *L. angarae*, *Miomeryx altaicus*, and *Gobiomeryx dubius*), carnivores (*Ardynictis furunculus*, *Hyaenodon eminus*), rodents (*Ardynomys olseni*), and others (Dashzeveg, 1974, translated from Russian). This faunal association is very similar to that listed by Berkey and Morris (1927, p. 363). If all the fossils collected by the Central Asiatic Expedition did indeed come from the "Middle Member," then the type of *S. avitum* would have originated stratigraphically somewhat lower than LPGIN 21-(1).



FIG. 1. Maps of chalicothere localities in Mongolia and China mentioned in the text.

Radinsky (1964b) described the stratigraphic section at Urtyn Obo (Baluch Camp) in the Shara Murun region of Inner Mongolia. The new specimens described in the present paper are from this locality. Radinsky (1964b, p. 10) used the *Schizotherium* maxillae (AMNH 26061) as an example of possible inaccurate recording of stratigraphic data from these beds; the anterior part of the right maxilla (Field no. 733 with P²-P³, see fig. 3) was recorded as coming from the base of the "Upper Red," whereas the posterior part of the same maxilla (Field no. 738, with P⁴-M³) was recorded as from the "Middle White." Radinsky concluded that errors in determining or recording the source of the material might have been due to drift of eroded material down the steep slopes.

Radinsky also noted that lithic correlations with type sections of the Shara Murun, Ulan Gochu, and Baron Sog formations are not available for the beds at Urtyn Obo. Correlation of the "Ulan Gochu" beds (from which AMNH 26061 comes) at Urtyn Obo with the type section of the Ulan Gochu Formation at Baron Sog Mesa is based on biostratigraphic evidence. Dawson (1968, p. 2) cited some of the uncertainties in faunal correlation using small mammals from the "Ulan Gochu" beds, Ulan Gochu Formation, and Ardyn Obo Formation. While noting the need for further work, she retained an early Oligocene designation for all three. Several species, for example *Ardynia praecox* (see Radinsky, 1967), *Parabrontops gobiensis* (see Granger and Gregory, 1943), and *?Ardynomys*

olseni (see Dawson, 1968), and a number of genera are found in both the Ardyn Obo Formation and the Ulan Gochu Formation (and/or equivalents). The presence of *Schizotherium avitum* in both the Ardyn Obo Formation and "Ulan Gochu" beds is therefore not unexpected. AMNH 103336 was also collected from Urtyn Obo, from "Baron Sog" beds. The same stratigraphic questions applying to material from the lower (= "Ulan Gochu") beds also pertain to this specimen. The Baron Sog Formation overlies the Ulan Gochu Formation at its type locality, and its fauna is generally considered to be early to medial Oligocene.

The Mc III (AMNH 26188) figured by Colbert (1934) and referred to *Schizotherium* sp. was presumed to be from "Baron Sog" beds at Nom Khong Shireh (= Nomogen Ora of Chow and Rozhdestvensky, 1960), Holy Mesa, in the Shara Murun region of Inner Mongolia. Again, the deposits from which this specimen came are only biostratigraphically correlated with the type section of the Baron Sog Formation. Comparison of this specimen with Mc III of *Schizotherium priscum* (no complete Mc III of any other *Schizotherium* species has been described) confirms its referral to *Schizotherium*. It is similar to Mc III of *S. priscum* in having a narrow proximal facet for Mc II and two facets for Mc IV but differs in its more symmetrical distal end. Because no postcranials unquestionably referred to *S. avitum* are known, specific assignment of AMNH 26188 is impossible.

Recent collecting in the Gungang Formation of the Baise District, Kwangsi, Peoples' Republic of China, by the Chinese Institute of Vertebrate Paleontology and Paleoanthropology uncovered chalicotheres material referred by Zhang (1976) to *Schizotherium nabanensis*, new species, and *Schizotherium* sp. Tang, You, Xü, Qiu, and Hu (1974) gave a tentative list of Gungang fossils and estimated the age of the fauna as late Eocene to Oligocene. Zhang suggested an (early?) Oligocene age.

Additional material referred to *Schizotherium* by various authors is cited from: St.-Jacques (on the east bank of the Huangho River within the city of Shanshenkon), Ordos region, Inner Mongolia Autonomous Region, Peoples' Republic of China (Teilhard, 1926), Taben-buluk

badland, Tieh-chiang-ku, Yindirte Valley, western Kansu, Peoples' Republic of China (Bohlin, 1946), and Tatal-Gol, Tsagan-Nor basin, about 300 miles (486 km.) southwest of Ulan Bator, Mongolian Peoples' Republic (Belyaeva, 1954). Mellett (1968) noted that Tatal-Gol is the same locality as the "Grand Canyon" area, from which much of the material from the Hsanda Gol Formation collected by the Central Asiatic Expeditions of 1922 and 1925 was derived. Mellett suggested a Rupelian age for the Hsanda Gol fauna. He also noted that the faunas from St.-Jacques and Taben-buluk are similar to the Hsanda Gol fauna, "but are somewhat sparser and probably younger." Some of the chalicotheres material from St.-Jacques figured by Teilhard (1926) is referable to the Chalicotheriinae (see below), which is not known elsewhere in Eurasia until the Aquitanian (*Chalicotherium wetzleri* of western Europe) or Burdigalian (*C. pilgrimi* from the Bugti beds of Pakistan). The faunas containing Tatal-Gol, Taben-buluk, and St.-Jacques chalicotheres appear to be distinctly later in age than those from the Ardyn Obo, "Ulan Gochu," and "Baron Sog" formations.

Hu (1959) described isolated teeth referred to *Schizotherium avitum* and *S. ordosium* from Oligocene deposits of the Ho-tau region, Inner Mongolia Autonomous region, Peoples' Republic of China. More precise information concerning locality, faunal associations, and age was not given. According to my information sources, the Ho-tau region covers roughly the same area referred to by Teilhard (1926) and others as Ordos, bounded on the west, north, and east by the Huang-ho River as it curves into Inner Mongolia. Teilhard's (1926) Saint-Jacques locality also lies in this region.

Descriptions of New Material. Because AMNH 20385 was not previously referred to *Schizotherium avitum*, it is described here, despite having been figured and discussed by Matthew and Granger (1925) and Colbert (1934). The molariform structure of the single preserved lower tooth led Matthew and Granger to suggest that this might be M_1 of a very small chalicotheres. However, this tooth is probably a deciduous tooth in the shallow mandibular ramus of a juvenile; both Matthew and Granger

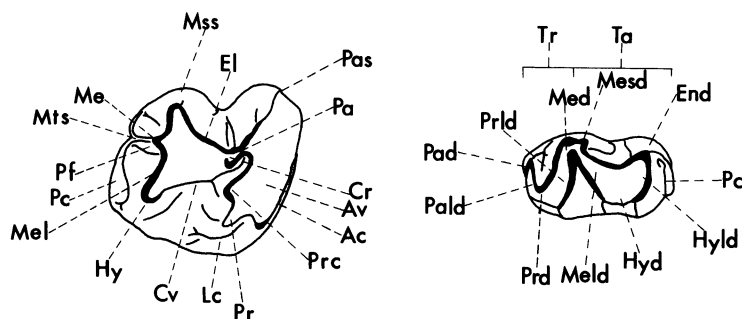


FIG. 2. Diagrammatic M^3 of AMNH 26061 and M_1 of AMNH 103336 (see fig. 3), showing dental structures mentioned in the text. Abbreviations: Ac - anterior cingulum, Av - anterior valley, Cr - crista, Cv - central valley, Ec - ectoloph, End - entoconid, Hy - hypocone, Hyd - hypoconid, Hyld - hypolophid, Lc - lingual cingulum, Me - metacone, Med - metaconid, Mel - metaloph, Meld - metalophid, Mesd - metastylid, Mss - mesostyle, Mts - metastyle, Pa - paracone, Pad - paraconid, Pald - paralophid, Pas - parastyle, Pc - posterior cingulum, Pf - postfossette, Pr - protocone, Prc - protoconule, Prd - protoconid, Prl - protoloph, Prld - protolophid, Ta - talonid, Tr - trigonid.

(1925) and Colbert (1934) made a tentative identification as dp_3 , and in view of the size of the tooth and the alveoli behind it compared with deciduous lowers of *S. priscum* and permanent teeth of *S. avitum* (see table 1) the assessment of those authors was not unreasonable. However, the paralophid of this tooth extends rather directly with only gradual curvature from protoconid to paraconid, as occurs on permanent lower molar teeth. Dp_3 of chalicotheriids (including specimens of *S. priscum* from the Phosphorites, see Stehlin, 1905, fig. 14) has a long paralophid which extends anteriorly from the protoconid and then makes a sharp bend to extend lingually toward the paraconid. As thus identified, dp_4 of AMNH 20385 is considerably smaller than the known dp_4 of *S. priscum*. It is very little worn and resembles permanent molars of AMNH 103336 from Urtyn Obo (see below) in having a transversely broad, though small, posterior cingulum. The metastylid is much lower than the metaconid and is more like a bulge on the posterior wall of the metaconid than a separate cuspid. No lingual fissure between metaconid and metastylid is visible. The lingual end of the metalophid clearly does not reach the metaconid/metastylid.

AMNH 26021 (fig. 3) represents left and right maxillae of a rather old individual whose

first and second molars were almost obliterated by wear. Among skull landmarks that are preserved is the anterior part of the ridge which continues (in complete specimens) posteriorly as the zygomatic arch. This ridge has its anterior origin opposite the mesostyle of M^2 . On the palate, the anterior border of the internal nares is opposite the lingual opening of the central valley on M^3 . The length of P^2 - M^3 on the right side is 91.4 mm.; other measurements are given in table 2.

M^3 of AMNH 26061 is slightly longer than wide and is clearly wider anteriorly than posteriorly. Although the tooth is not especially high-crowned, the ectoloph has only a slight lingual slant, and both paracone and metacone lie easily within the labial half of the tooth. Both parastyle and mesostyle are strongly developed; the metastyle is relatively weak. Between parastyle and mesostyle the ectoloph shows elongation, and there is a strong labial rib opposite the paracone. Although wear has opened the mesostyle lingually, it is clear that the metacone lay very close to the mesostyle in the unworn state. The part of the ectoloph between metacone and metastyle is very short and is directed anteroposteriorly. Wear on the tooth is restricted to the lingual surface of the ectoloph anterior to the metacone and to the anterior surfaces of both protoloph and metaloph.

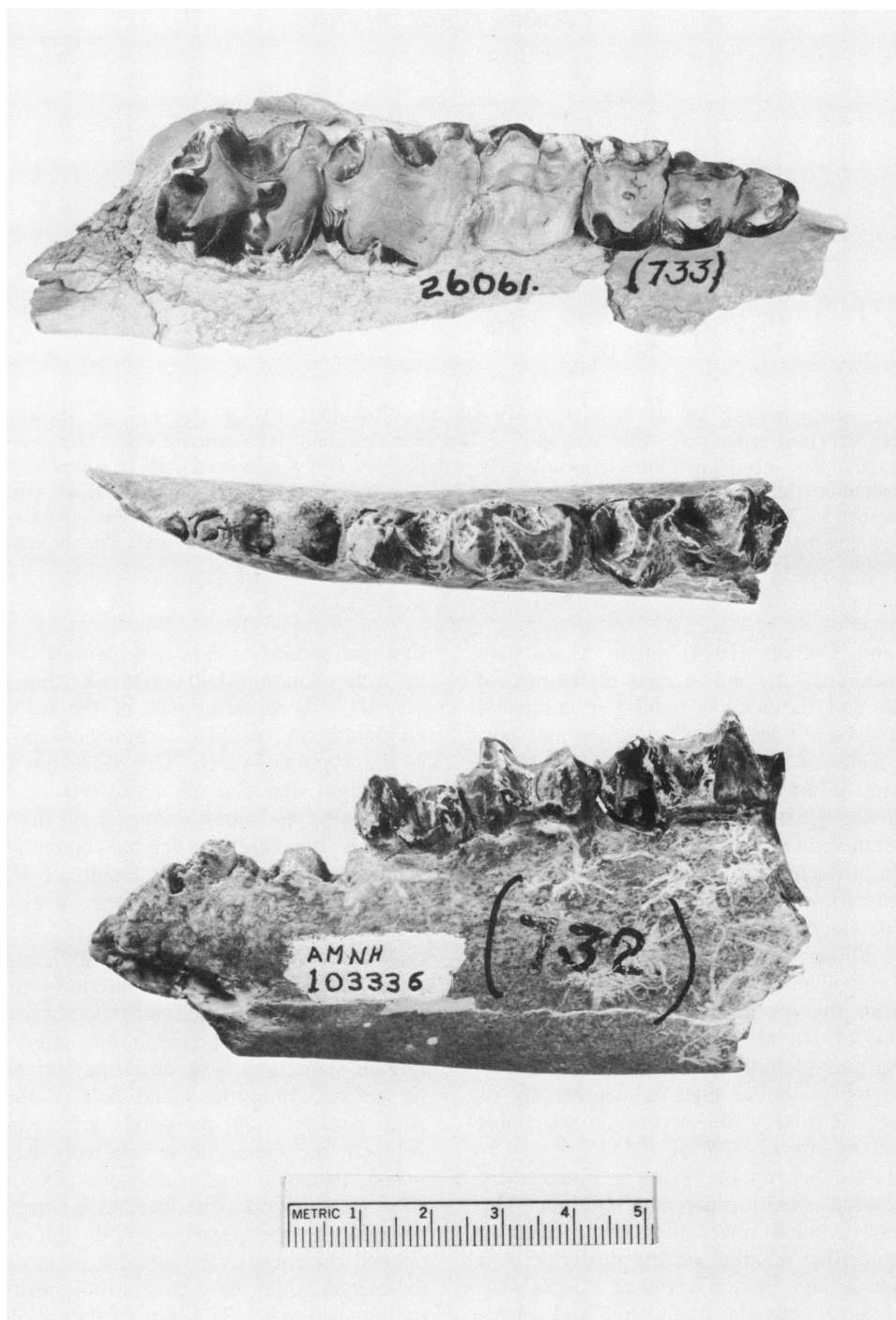


FIG. 3. Top: Occlusal view of right upper cheek teeth, P^2 - M^3 , of *Schizotherium* cf. *S. avitum*, from "Ulan Gochu beds" at Urtyn Obo, Inner Mongolia Autonomous Region, Peoples' Republic of China. Middle and bottom: Occlusal and labial views of AMNH 103336, P_4 - M_2 , *Schizotherium* cf. *S. avitum*, from "Baron Sog beds" at Urtyn Obo. Natural size.

Despite wear, the low protoloph is still complete, linking the paracone with protocone via a weak protoconule. The protocone is sharp-tipped, and its base is not greatly expanded. It is only slightly posterior to the paracone, and the protoloph is thus able to pass almost directly labially from the paracone to join the protocone at its anterolabial edge. There is no connection between the protoloph and cingulum at the anterolingual border of the protocone. Compared with the protoloph, the metaloph is

quite tall. The hypocone is taller than the general level of the metaloph, and its lingual and posterior edges are steep with no accessory cusps. The anterior cingulum, which runs between the parastyle and the anterolingual edge of the protocone, is clearly developed but not especially prominent, and the anterior valley, which it helps to enclose, is fairly small.

The lingual cingulum is interrupted opposite both protocone and hypocone and is weak opposite the lingual opening of the central valley.

TABLE 1

Measurements (in Millimeters) of Lower Cheek Teeth of *Schizotherium*. Some Values Taken from Borissiak (1921), Teilhard (1926), Bohlin (1946), Gabunia (1951), Hu (1959), Dashzeveg (1974), Zhang (1976)

	AMNH 19157 <i>S. avitum</i> holotype	LPGIN 21-(1) <i>S. avitum</i>	AMNH 20385 <i>S. avitum</i>	AMNH 103336 <i>Schizotherium</i> cf. <i>S. avitum</i>	<i>S. nabanensis</i> holotype	<i>Schizotherium</i> sp. Zhang, 1976
dp ₃ length	—	—	—	—	—	—
trigonid width	—	—	—	—	—	—
talonid width	—	—	—	—	—	—
dp ₄ length	—	—	16.3	—	—	—
trigonid width	—	—	7.9	—	—	—
talonid width	—	—	8.6	—	—	—
P ₂ length	—	—	—	—	13	—
maximum width	—	—	—	—	8	—
P ₃ length	—	—	—	—	—	—
maximum width	—	—	—	—	—	—
P ₄ length	—	14	—	15.9	16.2	—
maximum width	—	10	—	10.8	10.3	—
M ₁ length	—	17	—	20.8	—	15
trigonid width	—	9.5	—	10.7	—	—
talonid width	—	10	—	11.5	11.4 ^a	9.1 ^b
M ₂ length	—	22	—	28.0	27.7 ^a	—
trigonid width	—	11	—	13.0	13.1	—
talonid width	—	11	—	12.8	13.4	9.4
M ₃ length	26.0	26	—	—	—	—
trigonid width	12.2	12	—	—	14	11.5
talonid width	12.1	11.5	—	—	—	—
P ₂ - P ₄ length	—	—	—	44.5 ^a	40 ^a	—
M ₁ - M ₃ length	—	65	—	—	72 ^a	—
P ₂ - P ₄ length	—	—	—	—	0.56	—
M ₁ - M ₃ length	—	—	—	—	—	—

^a Approximate. ^b Only one width measurement given.

TABLE 1 — (Continued)

<i>S. chucuae</i> holotype	<i>S. turgaicum</i> Borissiak, 1921	AMNH 10495 cast <i>S. priscum</i>	AMNH 11077 <i>S. priscum</i>	<i>S. priscum</i> Mus. Natl. Hist. Nat. Paris - uncatalogued	? <i>Schizotherium</i> sp. (Bohlin, 1946)	<i>Schizotheriinae</i> indet. (Teilhard, 1926)	<i>S. ordosium</i> holotype
—	—	—	—	17.5	—	—	—
—	—	—	—	7.4	—	—	—
—	—	—	—	8.2	—	—	—
—	—	—	—	20.1	—	—	—
—	—	—	—	9.6	—	—	—
—	—	—	—	9.3	—	—	—
—	—	10.7	—	—	13.7	15	—
—	—	7.0	—	—	7.2	—	—
16.0	—	15.4	—	—	16.3	21	—
—	—	9.6	—	—	11.5	—	—
15.0	15	15.3	—	—	17.8	20	17 ^a
—	9	11.7	—	—	12.6	—	12
18.5	18.5	20.2	—	—	?17	25	22 ^a
—	—	13.4	—	—	—	—	—
—	10 ^b	13.7	—	—	14.0 ^b	—	15 ^b
24.5	23	26.6	—	—	25.1	32	—
—	—	14.0	—	—	—	—	—
—	12 ^b	14.4	—	—	17.0 ^b	—	—
29.8	—	28.1	29.9	—	27.4	—	33
14.5	—	15.0	15.2	—	—	—	—
13.9	—	14.2	14.3	—	17.2 ^b	—	16 ^b
—	—	41 ^a	—	—	49	54.6	—
72.8	—	75.8 ^a	—	—	70	91.9	—
—	—	0.54 ^a	—	—	0.70	0.59	—
—	—	—	—	—	—	—	—

Because the protocone has a less enlarged base than that of most other chalicotheriids, the central valley is relatively large. A small trace of a crista, running into the central valley from the ectoloph near the paracone, remains. A pronounced cingulum connects the bases of the hypocone and metastyle and forms a low posterior border for the postfossette. A much weaker cingulum connects the bases of the mesostyle and metastyle.

P²-P⁴ of AMNH 26061 are very worn; on P³ and P⁴, wear along protoloph, metaloph, and the lingual side of the ectoloph has merged to nearly obscure the central valley. The protoloph

and metaloph are worn almost equally, and both are worn more than the tip of the protocone. The ectoloph on P³ and P⁴ is straight; its highest point is the paracone, which is positioned about halfway along the anteroposterior length of each tooth. The parastyle is somewhat larger than the metastyle, but neither is especially strong. The best developed cingula on P³ and P⁴ are anterior and posterior to the protocone, but neither is so pronounced, nor are the valleys separating these cingula from the protocone so well-defined, as in other schizotheriines. P² is a small, triangular tooth, wide posteriorly and tapering to a narrow apex

at the low parastyle. The paracone is the tallest cusp, followed by the protocone. Although the surface of the tooth is obscured by wear, the metaloph seems to be better developed than the protoloph, though a low narrow protoloph, separate from the cingulum and connecting paracone and protocone, does appear to be retained. An anterior cingulum is present but is very weak.

P₄-M₂ of AMNH 103336 are somewhat worn and broken, but there are several characters worthy of note. M₂ is more than twice as long as its maximum width, and its trigonid is

slightly wider than the talonid. M₁ is not twice as long as wide, and its talonid is slightly wider than the trigonid (see table 1). M₁ is the only tooth in which the metaconid/metastylid is fully preserved. The metastylid is separate from the metaconid but only very weakly; there is only a very slight lingual depression between the two cuspids. The metaconid is slightly taller than the metastylid. The metalophid does not quite reach the metastylid but terminates slightly labial to the metaconid/metastylid. On M₁ there is a weak posterior cingulum, but the posterior cingulum on M₂ is both prominent

TABLE 2
Measurements (in Millimeters) of Upper Teeth of *Schizotherium*

	AMNH 26061 <i>Schizotherium</i> cf. <i>S. avitum</i>	AMNH 10411 cast <i>S. priscum</i>	AMNH 10494 cast <i>S. priscum</i> (Mus. Hist. Nat. Lyon)	PIN 2259-330 <i>S. turgaicum</i>	<i>Schizotherium</i> cf. <i>S. avitum</i> , Hu, 1959
dp ² maximum length	—	—	—	14.0 ^b	—
maximum width	—	—	—	12.4 ^b	—
dp ³ maximum length	—	—	18.0 ^a	17.1 ^b	—
maximum width	—	—	17.4 ^a	14.5 ^b	—
dp ⁴ maximum length	—	—	19.7 ^a	19.6 ^b	—
maximum width	—	—	18.3 ^a	16.7 ^b	—
P ² maximum length	9.2	13.0	—	—	—
maximum width	10.0	12.3	—	—	—
P ³ maximum length	10.8	15.0	—	—	—
maximum width	12.7	15.5	—	—	—
P ⁴ maximum length	11.3	15.3	—	—	—
maximum width	15.8	17.8	—	—	—
M ¹ maximum length	—	23.9	22.6 ^a	—	—
maximum width	—	21.8	20.1 ^a	—	—
M ² maximum length	21.8	—	22.8 ^a	—	27
maximum width	23.7	—	22.0 ^a	—	27
M ³ maximum length	23.1	—	—	—	—
maximum width	24.0	—	—	—	—
P ² - P ⁴ length	30.8	—	—	—	—
M ¹ - M ³ length	60.9	—	—	—	—
$\frac{P^2-P^4}{M^1-M^3}$ length ratio	0.51	—	—	—	—

^aIdentification debated, may represent dp³ - M³.
^bIdentification debated, may represent dp³ - M¹, dp².
Measurements approximate.

and broad. There is a weak labial and no lingual cingulum on these teeth.

Notes and Comparisons. AMNH 20384, a right mandibular ramus with P_2 , M_1 , and very worn dp_3 and dp_4 from the Ardyn Obo Formation, was referred to *Schizotherium avitum* by Matthew and Granger (1925) and used in the diagnosis of *S. avitum* by Belyaeva (1954). The teeth are not in good condition, but careful study of them suggests that they do not pertain to *S. avitum* or even to a chalicotheriid. Earl Manning (personal commun.), who has spent some time reexamining materials from the Central Asiatic Expeditions, suggests that AMNH 20384 pertains to an anthracotheriid; Matthew and Granger (1923) already indicated the presence of this family in the Ardyn Obo fauna.

Schizotherium nabanensis, recently named by Zhang (1976) for a mandibular ramus fragment with complete P_2 , P_4 , and M_2 (partial M_1 , M_3) from Kwangsi, is included below in the comparison with *S. avitum*. However, the holotype is hard to evaluate because it is incomplete and rather worn. In view of the dental variation which seems to occur within *S. avitum*, it is hard to find consistent differences between *S. avitum* and *S. nabanensis* (see below). More information is needed to determine whether these are indeed distinct species.

Hu (1959) named *Schizotherium ordosium* from the Ho-tau region of Inner Mongolia, and Zhang (1976) compared this species with *S. nabanensis*. Although closer geographically to *S. avitum* than any other *Schizotherium* species, *S. ordosium* is distinct morphologically (see below and table 3). Hu (1959) also referred the specimens from Saint-Jacques described by Teilhard (1926) to *S. ordosium*, partly because of similarly large size (see table 1). However, several problems surround Teilhard's specimens, and they are here treated separately.

Dashzeveg (1974), following Matthew and Granger (1923), Belyaeva (1954), and his own evidence, diagnosed *Schizotherium avitum* as follows: "size somewhat smaller than in *S. priscum* from the Oligocene of France (Quercy); trigonid and talonid of P_4 - M_3 almost equal in width; length of M_3 more than twice exceeds its width; metastylid of M_3 clearly separated at the tip from the metaconid; hypoconulid weakly developed; cingulum absent on

the lingual side, weakly developed on the labial side of the molar teeth" (translated from Russian). Each of these points is discussed below, and comparisons among *Schizotherium* species are summarized in table 3.

Size: Any comparison of size among *Schizotherium* species must take into account the size sexual dimorphism prevalent among chalicotheriids and specifically noted elsewhere for *S. priscum* (Coombs, 1975, p. 59). Known *Schizotherium* specimens have suggested that "average" size of dental remains is largest in *S. ordosium*, large in *S. priscum* and *S. chucuae*, smallest in *S. avitum*, and intermediate in *S. turgaicum* (known dental size in *S. turgaicum* is not consistent with the larger postcranial remains presently known, as was noted by Coombs, 1976, p. 193). The type of *S. nabanensis* is approximately as large as specimens of *S. priscum* and *S. chucuae*. However, isolated lower molars from the same formation, referred by Zhang (1976) to *Schizotherium* sp. but morphologically comparable with the type of *S. nabanensis*, are much closer in size to *S. avitum*. Of *S. avitum* specimens, AMNH 19157 (the holotype), LPGIN 21-(1), and AMNH 20385 are small; among questionably referred specimens, AMNH 26021 is also small, whereas AMNH 103336 is larger, similar in size to the type of *S. nabanensis*, and approaching the size of *S. priscum* (see tables 1, 2). *Schizotherium avitum* may indeed be the smallest *Schizotherium* species, but it is at least equally possible that most of the known specimens are females. A large size range is probably acceptable in *S. avitum* as well as in other *Schizotherium* species.

Trigonid and talonid width: *Schizotherium priscum*, *S. chucuae*, and *S. ordosium* have a wider trigonid than talonid on M_3 , whereas *S. avitum* has M_3 trigonid and talonid of subequal width (a complete M_3 has not been described for *S. turgaicum*, or *S. nabanensis*). Trigonid and talonid of more anterior molars seem to have subequal width in all *Schizotherium* species. AMNH 19157 and LPGIN 21-(1) have subequally wide M_3 trigonid and talonid; M_2 dimensions of AMNH 103336 suggest that the M_3 trigonid might have been wider in this animal.

Length versus width of M_3 : M_3 of *S. avitum*

TABLE 3
Comparison of Lower Cheek Teeth of Six *Schizotherium* Species
Data from Borissiak (1921), Gabunia (1951), Belyaeva (1954), Hu (1959), Dashzeveg (1974),
Zhang (1976), and Personal Observation

	<i>S. avitum</i>	<i>S. priscum</i>	<i>S. turgicum</i>	<i>S. chucuae</i>	<i>S. nabanensis</i>	<i>S. ordosium</i>
Known lower teeth	P ₄ - M ₃	All teeth	P ₄ - M ₂ 1 specimen	P ₃ - M ₃ (partial) 1 specimen	P ₄ - M ₃ (partial) 1 specimen	P ₄ , M ₁ , M ₃
Relative Size (known average)	Small	Large	Intermediate	Large	Large	Very large
Trigonid wider than talonid?	No	Yes (M ₃)	No?	Yes (M ₃)	No?	Yes (M ₃)
Length M ₂ , M ₃ >2× maximum width?	Yes	No	No	Yes M ₃ , ?M ₂	Yes	Yes
Development of separate metastylid	Weak on holotype, but variable	Strong	Strong	Very weak	Some (unclear because of wear)	Strong
M ₃ hypoconulid	Small, narrow	Well developed, broad	M ₃ not known	Very small	M ₃ talonid not known	Well developed
Molar cingula (especially posterior cingulum)	Variable, but not strong	Well developed	Well developed	Very weak	Well developed	Unclear, not strong
Metalophid merges with metastylid?	No	Yes	No	No	?	?
Known geographic range	Mongolia, northern China	Western Europe	Kazakhstan, U.S.S.R.	Georgia, U.S.S.R.	Southern China	Northern China

(AMNH 19157, LPGIN 21-(1), and M₂ of AMNH 103336), M₃ of *S. chucuae* (holotype), M₃ of *S. ordosium* (holotype), and M₂ of *S. nabanensis* (holotype) are more than twice as long as their greatest width. M₃ of *S. priscum* is a relatively wider tooth (M₃ less than twice as long as wide), and dimensions of M₂ suggest that M₃ of *S. turgicum* might also be relatively wide. Anterior to M₂ the length/width ratio for cheek teeth becomes less than two in all species.

Metastylid separation from metaconid: LPGIN 21-(1), as figured and described by Dashzeveg (1974), has an M₃ metastylid nearly as tall as the metaconid and separated from the metaconid at its tip by a distinct fissure. However, a distinct metastylid is not a universal development for *S. avitum*, because the holotype, AMNH 19157, has a very weak

metastylid with barely a hint of a fissure separating it from the metaconid (this tooth is, however, slightly worn). The lower molar referred by Hu (1959) to *S. avitum* has a very weak metastylid, as do AMNH 20385 (dp₄) and AMNH 103336 (see descriptions above). Some degree of variation in metastylid development is not surprising, for Butler (1965) noted such variation in lower molars of *Chalicotherium rusingense*. A relatively tall metastylid, separated from the metaconid by a deep fissure, is present in known specimens of *S. ordosium*, *S. nabanensis*, *S. priscum*, and *S. turgicum*. The holotype of *S. chucuae* has an extremely weak metastylid; it is, according to Gabunia (1951) weaker than in any other *Schizotherium* species.

M₃ hypoconulid: An important character of the holotype of *S. avitum* is the short, narrow

M₃ hypoconulid. A narrow hypoconulid also occurs on M₃ of LPGIN 21-(1), though figures of this tooth by Dashzeveg (1974) suggest that the hypoconulid was slightly more prominent than in the holotype. It is interesting also to observe on Dashzeveg's figure of LPGIN 21-(1) that the posterior cingulum of M₂ is fairly prominent and much broader transversely than the hypoconulid on M₃. This cingulum suggests that the broad posterior cingulum on AMNH 20385 (dp₄) and AMNH 103336 (M₂) does not necessarily disqualify these specimens from reference to *S. avitum*, nor does the well-developed posterior cingulum on M₂ of *S. turgaicum* necessarily imply that M₃ of that species would have a large hypoconulid. *S. priscum* has a large, broad M₃ hypoconulid, but *S. chucuae* has a very weak one, comparable to the hypoconulid of *S. avitum* or even weaker (Gabunia, 1951). *S. ordosium* has a well-developed M₃ hypoconulid (Hu, 1959, pl. 1, fig. 7).

Lower molar cingula: Generally speaking, *Schizotherium* lower molars have no lingual cingula, weak labial cingula, and variable anterior and posterior cingula. According to Gabunia (1951), *S. chucuae* has the weakest cingula and *S. priscum* and *S. turgaicum* the strongest cingula. Zhang (1976) used stronger cingulum development in *S. nabanensis* and *Schizotherium* sp. from Kwangsi as a differentiating character from *S. avitum* and *S. ordosium*. M₂ of AMNH 103336 has a rather strong posterior cingulum, but it is difficult to determine how this cingulum compares with that of LPGIN 21-(1), in which M₂ is more worn and M₃ is crowded into the posterior margin of M₂. The degree of cingulum variation within *S. avitum* is still unclear.

Lingual contact of metalophid with metastylid: Both Gabunia (1951) and Belyaeva (1954) noted that the metalophid ends lingually against the protolophid without reaching the metastylid in *S. turgaicum* and *S. chucuae* but fully merges with the metastylid in *S. priscum*. In this respect, *S. priscum* resembles more advanced Schizotheriinae. In the holotype of *S. avitum* the metalophid does not quite contact the metastylid, and this pattern also holds in

AMNH 20385 and AMNH 103336. Lingual confluence or separation of the metalophid and metastylid is not clear in LPGIN 21-(1) as figured by Dashzeveg (1974) or in the holotype of *S. nabanensis* as figured by Zhang (1976) or *S. ordosium* as figured by Hu (1959).

From the preceding discussion it becomes clear that even if *S. avitum* were to be limited to the holotype and LPGIN 21-(1), some variation in degree of metastylid separation and, to a lesser degree, hypoconulid development would be evident. Nevertheless, *S. avitum* can, on present evidence, be differentiated from other *Schizotherium* species on the basis of a combination of characters: ?size, hypoconulid development, and molar proportions (see Diagnosis).

How should the additional material described in this paper be classified? AMNH 20385 (dp₄) resembles the *S. avitum* holotype in small size, poor separation of metastylid from metaconid, separation of metalophid lingual end from metastylid, and general proportions (exact correspondence of proportions cannot be expected between a dp₄ and a M₃). In view of the broad posterior cingulum on M₂ of LPGIN 21-(1), this character loses significance in a differentiation of AMNH 20385 from *S. avitum*. AMNH 20385 almost certainly can be referred to *S. avitum*. AMNH 26061, the upper dentition, is difficult to compare with known material of *S. avitum*. The only character available for comparison is size, which in the case of AMNH 26061 is smaller than compared with upper dentitions of other *Schizotherium* species. On the basis of small size, AMNH 26061 is probably referable to *S. avitum*. M³ of AMNH 26061 is in general quite comparable to M³ of *S. priscum* (see Coombs, 1976, fig. 3, for a relatively unworn M³ of *S. priscum*) and cannot be differentiated from it in any particular way. Both share a somewhat square shape with the beginning of ectoloph elongation between parastyle and mesostyle, paracone and metacone in labial half of tooth, labial ectoloph rib opposite paracone, crista present, protocone sharp and without strong posterior migration, and weak anterior cingulum. These general characters are also

shared with upper deciduous teeth of "*Kyzylkhippus orlovi*," Gabunia and Belyaeva (1964), now referred to *S. turgaicum* (Coombs, 1976). One difference of AMNH 26061 is that the premolars are proportionally shorter relative to the molars and broader compared with length than in known specimens of *S. priscum*. AMNH 103336 (P_4 - M_2) is a difficult specimen to place taxonomically. It resembles the holotype of *S. avitum* in weak metastylid, metalophid not confluent with metastylid, and molar length versus width (observed on M_2). It differs from the type primarily in larger size (similar to *S. priscum*, *S. chucuae*, or *S. nabanensis*), and its well-developed posterior cingulum on M_2 suggests a possible (but perhaps insignificant) further difference. This specimen does not appear to be referable to *S. priscum*, *S. turgaicum*, or *S. chucuae* (see table 3). Reference to *S. nabanensis* is suggested by some characters (size, cingulum development) and to *S. avitum* by others (small metastylid). Because size and cingulum development may be intraspecifically variable and the distinction between *S. avitum* and *S. nabanensis* is not altogether clear, AMNH 103336 is questionably referred to *S. avitum*.

Two isolated teeth from Ho-tau were referred by Hu (1959) to *S. avitum*. These specimens are considered as *Schizotherium* cf. *S. avitum* in the present paper. One of these teeth, which Hu (1959, pl. 1, fig. 4, No. V2402.1) identified as a left M^2 , is much larger than upper molars of AMNH 26061 (table 2) but otherwise resembles them in almost every particularity. The Ho-tau upper molar is much less worn than molars of AMNH 26061 and thus preserves such anatomical landmarks as the crista and protoconule more sharply. In view of the large size of this specimen (table 2) and absence of known good distinguishing features among *Schizotherium* upper molars, the possibility that this tooth belongs to *S. ordosium* must be reserved. A lower molar tooth, which Hu (1959, pl. 1, fig. 5, No. V2402.2) identified as M_3 , has a length of 24.5 mm. and a width of 12.5 mm. and is therefore small compared to M_3 of known specimens of *S. avitum*. Also, its length is slightly less than two times its width,

and the posterior cingulum is broad and therefore more reminiscent of the M_2 posterior cingulum of AMNH 103336 (fig. 3B,C) than of known M_3 hypoconulids of *S. avitum*. This tooth is more likely an M_2 than an M_3 . It resembles lower molars of *S. avitum* in having trigonid and talonid of subequal widths and in having a low metastylid which does not appear to be fully confluent with the metalophid.

It is very difficult on present evidence to understand relationships among *Schizotherium* species. None of the species is known from any quantity of material. *Schizotherium priscum* is the best known, but even here the degree of intraspecific variation is hard to determine. The only part of the body that can be compared for all species is the lower cheek teeth. Unfortunately, my own studies of *Moropus*, including a relatively large sample of *M. elatus*, suggest that considerable intraspecific variation is common in chalicotheriid dentitions and that consistent differences between species are slight or nonexistent. Postcranial elements are more appropriate taxonomic indicators. A fuller knowledge of lower cheek teeth of all *Schizotherium* species may indicate that morphology of these teeth forms a broad interspecific continuum and is nearly useless for taxonomic purposes. Nevertheless, some present attempt at elucidation of relationships among *Schizotherium* species is instructive. Aside from *S. nabanensis*, which is poorly known but resembles *S. avitum* in a number of ways, *S. avitum* seems closest to *S. chucuae* on the basis of reduced metastylid and hypoconulid; such reduction is carried to an extreme in the holotype of *S. chucuae*. *Schizotherium priscum* is derived in comparison to the other *Schizotherium* species in having a metalophid which is confluent with the metastylid. In terms of lower cheek tooth morphology, *S. turgaicum* may be the least derived *Schizotherium* species, but postcranial characters, like the loss or reduction of the trapezium in the manus (see Coombs, 1976), suggest that *S. turgaicum* is not an especially primitive *Schizotherium* species. *Schizotherium ordosium*, the largest known *Schizotherium* species, resembles *S. priscum* in its wide M_3 trigonid but not in its

M_3 length/width proportions; the degree of confluence of metalophid and metastylid in *S. ordosium* is not clear from available figures.

SOME PROBLEMATIC MATERIAL

Teilhard (1926) referred fragmentary upper teeth, a mandibular ramus with cheek teeth, isolated anterior teeth, and phalanges from Saint-Jacques (see locality discussion above) to *Schizotherium* cf. *S. avitum*, but it is unlikely that any of the material belongs to this species. For one thing, the specimens far exceed in size material of *S. avitum* or even of *S. priscum* (dental lengths in mm.: P_2 - $P_4 = 55$, $P_2 = 15$, $P_3 = 21$, $P_4 = 20$, $M_1 = 25$, $M_2 = 32$, $M^{22} = 33$, $M^{73} = 35$). Teilhard's illustrations suggest that more than one kind of chalicotherine may be represented. The asymmetrical proximal phalanx which Teilhard figured in plate 3, figure 3, appears to represent a chalicotheriine, probably *Chalicotherium*. The canines (Teilhard, 1926: 18, fig. 8), if they belong to a chalicotherine, also more likely belong to a chalicotheriine than a schizotheriine (Coombs, In press). The other dental material and phalanges that Teilhard figured appear referable to a schizotheriine larger than *Schizotherium* and closer in size to a small *Moropus* species like *M. oregonensis*. Among characters which suggest that Teilhard's upper molars and lower cheek teeth are referable to the Schizotheriinae are: the tall upper molar ectoloph with paracone and metacone well in the labial half of the tooth, suggestion of ectoloph elongation between paracone and metacone, separate metastylid on lower molars (present also in primitive Chalicotheriinae), and long anterior part of jaw. The latter, probably primitive, character, which includes the length of the lower premolar row and the diastema anterior to P_2 relative to the molar row and the depth of the jaw, is extreme even within the generally long-faced Schizotheriinae. Unfortunately, the posterior part of M_3 is not preserved and the presence or absence of a hypoconulid cannot be determined. The strong anterior cingulum and anterolingual junction of the protoloph with the protocone figured by Teilhard suggest developments in later Schizotheriinae which are less expressed

in known *Schizotherium*. Hu's (1959) reference of the mandible from Saint-Jacques to *S. ordosium* may be correct, but for the present I regard Teilhard's material, with the exception of the proximal phalanx and canine mentioned above, as indeterminate Schizotheriinae.

It is also difficult to determine the affinities of the worn and somewhat damaged cheek teeth on a mandible from Taben-buluk, Kansu, figured and described by Bohlin (1946). This specimen is considerably smaller than the material described by Teilhard (1926), though larger than the type of *S. avitum* (see table 1). As with Teilhard's mandible, the anterior diastema and premolar row are quite long compared to the molar row. Bohlin's measurements suggest that the molars are much broader compared to their length than in *S. avitum*, *S. ordosium*, or even *S. priscum*. The M_3 trigonid is wider than the talonid. Damage to the posterior part of M_3 on both sides of this specimen poses difficulties in a comparison with *Schizotherium* species; Bohlin noted that M_3 hypoconulid development (apparently small) seems to vary from left to right. Figures of this specimen suggest that the worn metastylid was well-developed and continuous with the metalophid. Reference to *S. avitum* is unlikely; Bohlin's designation as ?*Schizotherium* sp. is still probably the best assessment of this specimen.

SUMMARY

The following specimens, all lower teeth from the Ardyn Obo Formation of the Mongolian Peoples' Republic, are referred to *Schizotherium avitum*: AMNH 19157 (M_3 holotype), LPGIN 21-(1) (P_4 - M_3), and AMNH 20385 (dp_4). AMNH 20384, a lower immature dentition previously considered to belong to *S. avitum*, is not a chalicotherine but probably an anthracotherine. AMNH 26061, upper cheek teeth from "Ulan Gochu beds" at Urtyn Obo, Inner Mongolia, Peoples' Republic of China, is questionably referred to *S. avitum*, as is AMNH 103336, lower teeth from "Baron Sog beds" at Urtyn Obo. Two isolated teeth from Ho-tau, Inner Mongolia, referred by Hu (1959) to *S. avitum*, are also questionably included in *S. avitum*.

Six species of *Schizotherium* are currently differentiated, primarily on the basis of size and lower cheek tooth morphology. Size sexual dimorphism and intraspecific dental variation common in chalicotheriids make such taxonomic use of the teeth risky, but few other aspects of *Schizotherium* structure are sufficiently known. *Schizotherium avitum* shows some variation in metastylid, posterior cingulum, and M_3 hypoconulid development and possibly in size. Nevertheless, *S. avitum* appears to represent a relatively small *Schizotherium* species, with subequally wide trigonid and talonid, M_2 and M_3 narrow compared to width, small metastylid, and small, narrow, M_3 hypoconulid. It resembles *S. chucuae* in metastylid and hypoconulid reduction and long, narrow, M_3 . *S. nabanensis* is also close to *S. avitum*, but neither species is well enough known to be clearly differentiable from one another.

Specimens from Saint-Jacques, Inner Mongolia, described by Teilhard (1926), appear to belong to two different chalicotheriids, one an indeterminate chalicotheriine, the other an indeterminate schizotheriine. Dental material described by Bohlin (1946) from Taben-buluk, western Kansu, seems to be referable to *Schizotherium*, but not to *S. avitum*.

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