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Artiodactyla from the Early Eocene of southern Kazakhstan

Artiodactyla aus dem Untereozän des südlichen Kasachstan

With 2 figures, 1 table and 1 plate

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Summary: New mammal remains are preliminarily described from the Lower Eocene of southern Kazakhstan. These are (i) a distal joint of a humerus and (ii) a mandible fragment from the Zhylga 1b and Zhylga 2 locality, found in 1996 by the first author. The specimens are referred to artiodactyls based on morphological comparisons to other Lower and Middle Eocene material, particularly from the Geiseltal near Halle (Germany). The humerus probably belongs to a diacodexeid. It displays one of the earliest phylogenetic stages in the formation of the elbow characteristic for artiodactyls. It represents an intermediate evolutionary stage between the species of *Diacodexis* and North American genera of the Lower Eocene such as *Bunophorus*. This is a further biostratigraphical indication for the Eocene age of Zhylga 1b and Zhylga 2. Therefore the significance of the Kazakhstanian fossil sites for the mammal radiation is stressed.

Zusammenfassung: Neue Fossilien von Säugetieren aus dem Unteren Eozän des südlichen Kasachstans werden vorläufig beschrieben. Es handelt sich um ein distales Humerusgelenk und ein Unterkieferfragment der Lokalitäten Zhylga 1b und Zhylga 2, welche 1996 vom Erstautor geborgen wurden. Nach morphologischen Vergleichen mit anderem unter- und mitteleozänen Material, insbesondere aus dem Geiseltal bei Halle (Deutschland), können die Stücke den Artiodactyla zugewiesen werden. Der Humerus gehört vermutlich zu einem Diacodexeiden. Er zeigt eines der frühesten phylogenetischen Stadien in der Umbildung des Ellenbogengelenkes bei den Artiodactylen und repräsentiert ein Entwicklungsniveau zwischen den Arten von *Diacodexis* und den Nordamerikanischen Gattungen des Untereozäns wie *Bunophorus*. Hiermit wird ein weiterer biostratigraphischer Hinweis für die Einstufung von Zhylga 1b in das Eozän gegeben und die Bedeutung der kasachischen Fundstellen für die Radiation der Mammalier unterstrichen.

1 Introduction

The origin and early evolution of the mammalian order Artiodactyla remains poorly understood. *Diacodexis*, the oldest known Early Eocene artiodactyl, was already highly cursorial and, in postcranial adaptations, close to tragulids and other primitive ruminants (ROSE 1982). Moreover, all known Early - Middle Eocene artiodactyls were uniformly highly adopted for cursorial - saltatorial locomotion (ROSE 1985). The early stages of this adaptation are still inadequately documented. Postcranial elements of Early Eocene artiodactyls were previously known only in *Diacodexis metsiacus* and *Bunophorus etsagicus*, both from the Wasatchian of North America (GUTHRIE 1968; ROSE 1985), and in *Diacodexis pakistanensis* from the Bumbanian of Pakistan (THEWISSEN & HUSSAIN 1990). We report here the discovery of an artiodactyl distal humerus fragment (Fig. 1) from the basal Eocene of southern Kazakhstan. The specimen comes from the Zhylga 1b locality, a white sand quarry near the Zhylga railway station in Chimkent Province. From the Zhylga 1a locality, which is stratigraphically lower, a diverse vertebrate fauna of latest Palaeocene age is known. It consists of chondrichthyan and osteichthyan fishes, choristoderes, sea turtles, sea snakes, birds, and mammals (NESSOV & KAZNYSHKIN 1983; NESSOV & UDOVICHENKO 1984; NESSOV 1987a und b, 1992; AVERIANOV et al. 1993; AVERIANOV 1995).

From the Zhylga 1b level a similar vertebrate fauna is known. It differs, however, by the occurrence of other dominant species among sharks and another genus of sea snake. Only two mammalian remains were discovered from this site by the first author in 1996: a glires incisor and the humerus fragment reported here. Another mammal fossil was found in the Zhylga 2 locality, 2 km east to the Zhylga railway station, and approximately 7 km - 8 km from the Zhylga 1 locality, see NESSOV (1992: fig.1). This is a dentary fragment of an artiodactyl, as described below. The vertebrate fauna from the Zhylga 2 locality consists of chondrichthyan and osteichthyan fishes, turtles, and birds. It is similar to the fauna from the Zhylga 1b level (unpublished data).

2 Morphological description

The following anatomical expressions for the bones correspond to NICKEL et al. (1992), the nomenclature of the teeth to ERFURT & HAUBOLD (1989: Abb. 1). The terms are used in a topographical, not in a phylogenetic sense. All indications of directions in measurements are in consensus with DRIESCH (1976). Material of the following institutions was used or referred to:

collection of the Geiseltalmuseum of the Martin-Luther University; Halle	GMH
collection of the Senckenbergische Naturforschende Gesellschaft; Frankfurt/Main	SMF
collection of the University of Colorado Museum; Boulder	UC
collection of the United States Geological Survey; Denver	USGS
collection of the Zoological Institute of the Academy of Sciences; St. Petersburg	ZIN

Specimen ZIN: 34493 (Fig. 1) Artiodactyla inc. sed.

The first specimen, coming from the Zhylga 2 locality, is a fragment of the left mandible with P/2, partial P/3 and alveoli of P/1. The P/2 is well developed, showing a massive and central protoconid. The length is 4.1 mm, the width exceeds 1 mm. The lingual side of the tooth is somewhat damaged. A smaller paraconid and hypoconid are developed, and a complete crest runs from the oral to the distal edge of the tooth. The larger P/3 with a width of approximately 1.2 mm is broken in the middle. The P/3 follows the P/2 without a diastema. The P/3 has a large protoconid with a worn crest similar to the P/2. The two alveoli in front of the P/2 are referred to P/1. They are different in size, with lengths of 0.7 mm and 0.9 mm. There is no diasteme between these premolars. The corpus mandibulae is relatively strong, with a height of 7.9 mm, measured below the border between P/2 and P/3. The foramen mentale occurs below P/2, with a diameter of 0.7 mm.

Specimen ZIN: 34492 (Fig. 2) Diacodexeidae indet.

The nearly complete distal end of a right humerus comes from the Zhylga 1b locality. It contains a small piece of the diaphysis. The surface of the bone is corroded by weathering. The total length of the specimen is 20.8 mm, the distal breadth 19.5 mm. The epicondylus medialis is narrow in mediolateral direction, lacking a foramen supracondylaris. The insertion surfaces for the carpal and digital flexors are small. The epicondylus lateralis is reduced, too. The brachial flange (crista humeri) is weak for the attachment of extensor, brachialis, and brachioradialis muscles. The capitulum is comparatively short and ellipsoid. Anteriorly, the lateral margin of trochlea raises into a sharp ridge bordering a well marked groove for the caput radii. The medial trochlear rim insignificantly projects distally beyond the capitulum. Inferiorly, the capitulum surface tapers posteromedially until it joins with the posterolateral crest of the olecranon fossa. The olecranon fossa is deeply excavated and perforated by a large ellipsoid supratrochlear foramen.

Figure 1:

Fossils from the Zhylga 1b and 2 locality, southern Kazakhstan; Lower Eocene (drawings by A. AVERIANOV, St. Petersburg).

A - C: Artiodactyl inc. sed., ZIN 34493, fragment of left dentary with P/2-3 and alveolus of P/1.
A: labial-, B: lingual-, C: occlusal-view.
D - H: Diacodexeid indet., ZIN 34492, fragment of right distal humerus.
D: anterior-, E: posterior-, F: medial-, G: lateral-, H: distal-view.

Figure 2:

Humeri of haplobunodontid artiodactyls from the Geiseltal near Halle (Germany); Middle Eocene (drawings by R. RAUSCH, Martin-Luther-University Halle), anterior and posterior view.

A - B: *Anthracobunodon neumarkensis* GMH XVIII-164b; fragment of right humerus.
C - D: *Haplobunodon mülleri* GMH XXII-553; fragment of right humerus.
E - F: *Anthracobunodon weigelti* GMH XXII-761; fragment of left humerus.

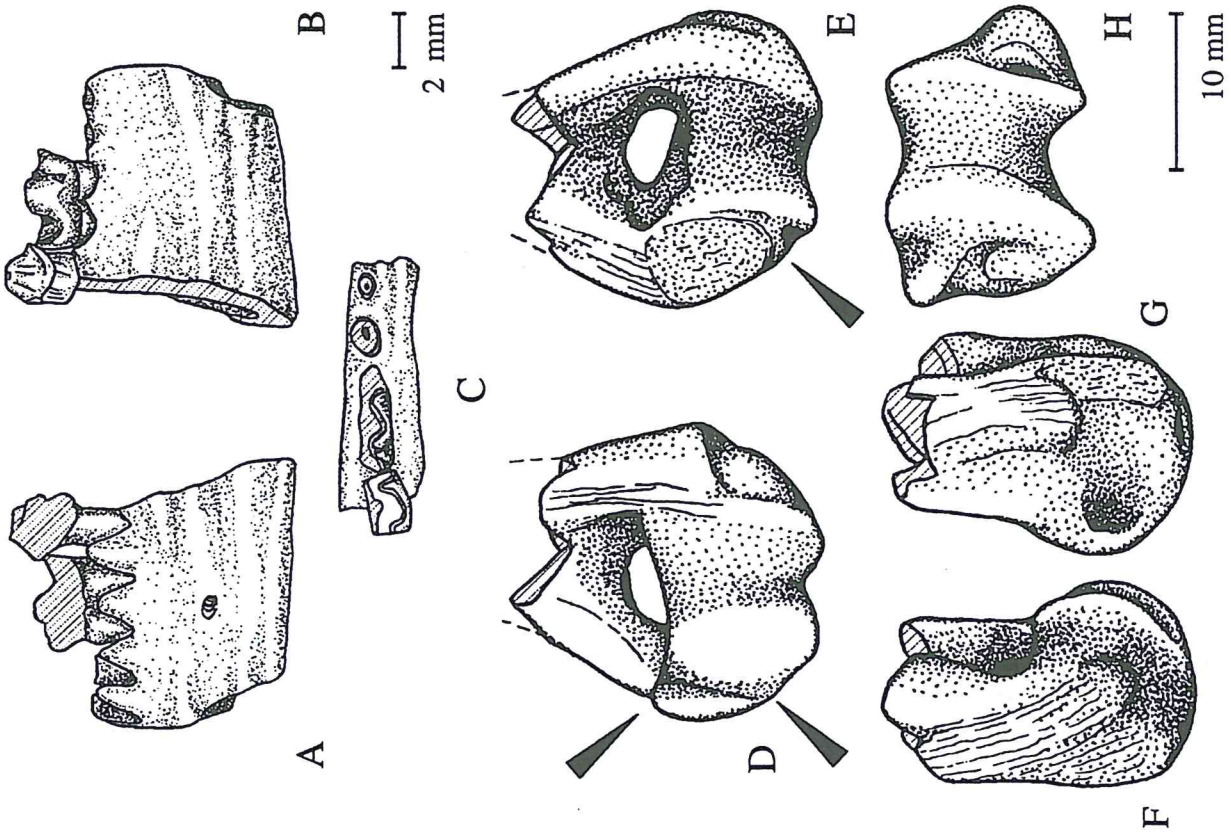

Figure 1

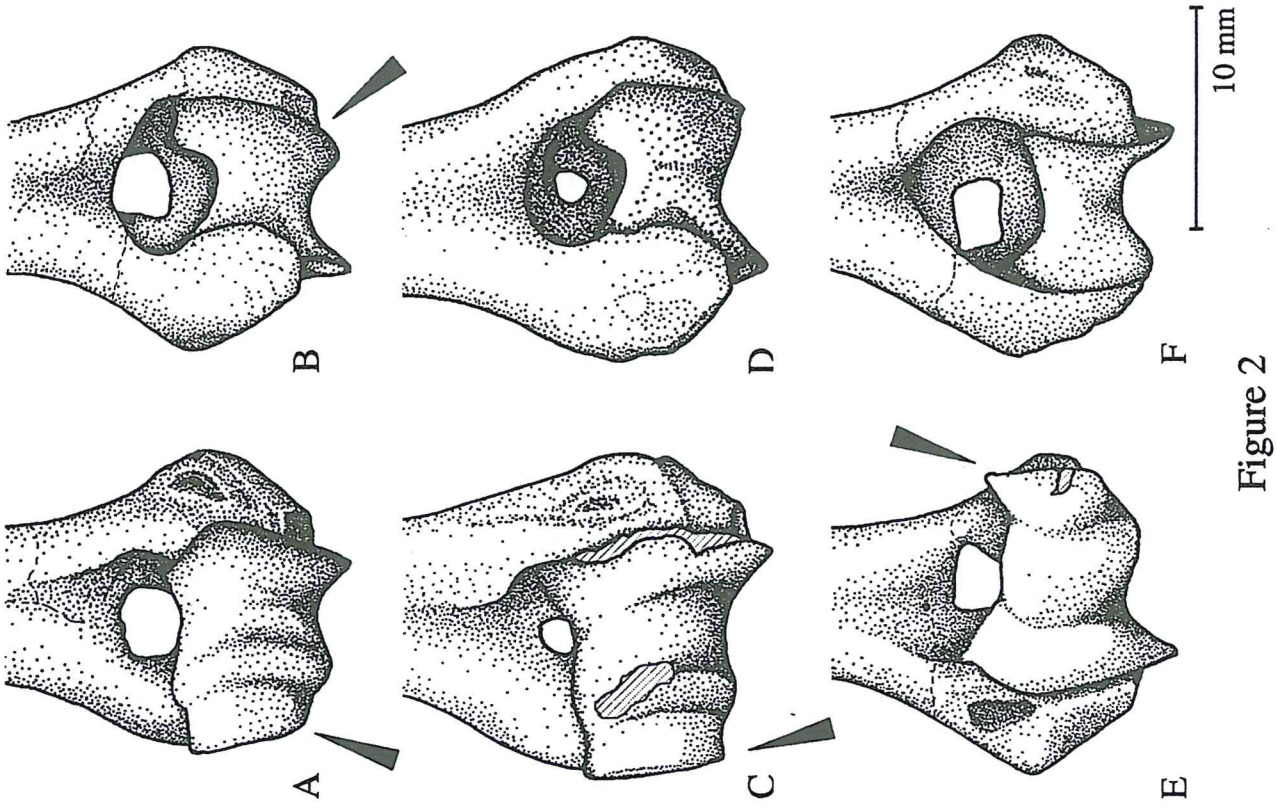

Figure 2

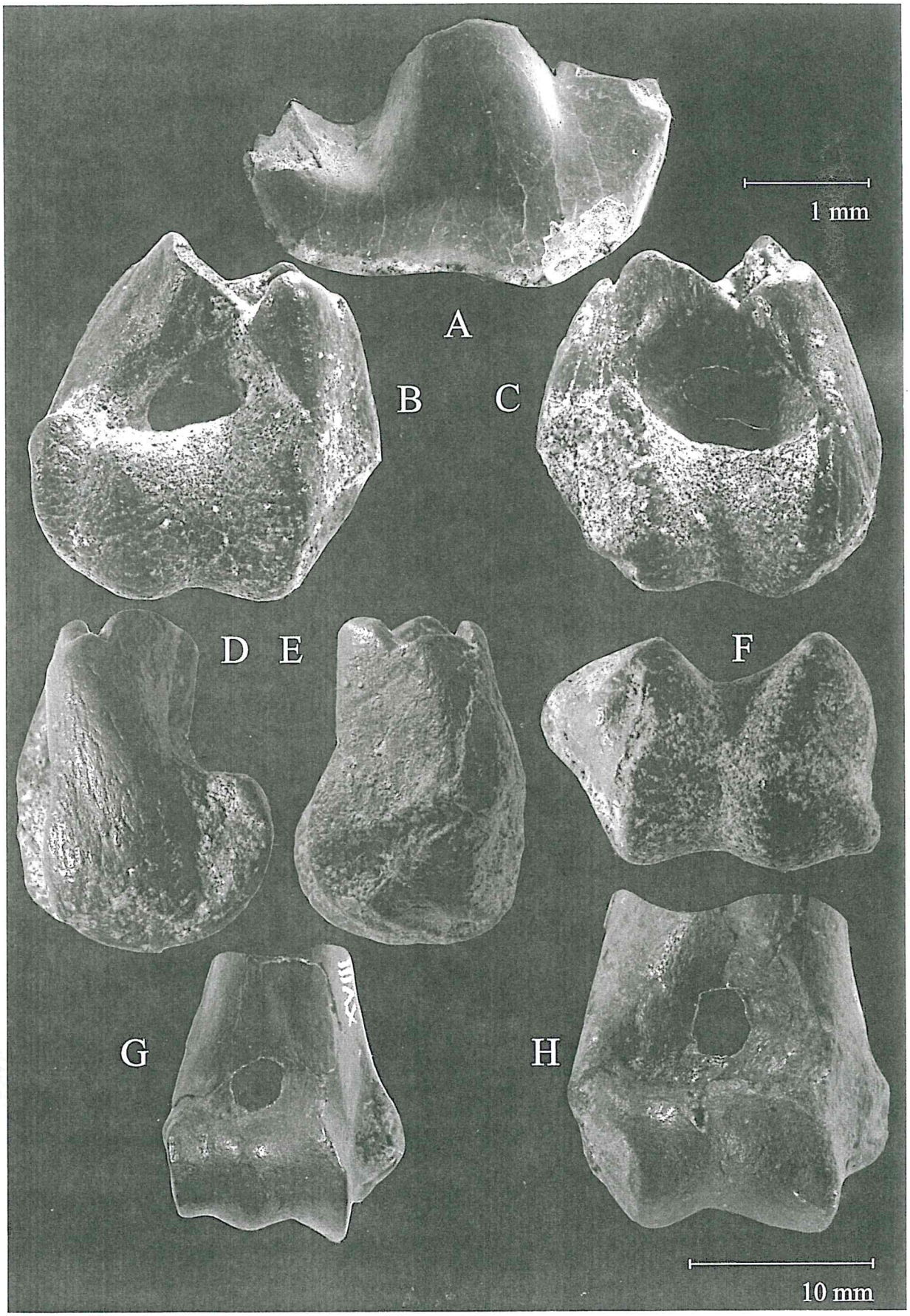
1 mm
A
B
C
D
E
F
G
H
10 mm

Plate 1:

Comparison of fossils from the Lower Eocene Zhylga 1b and 2 locality (southern Kazakhstan) to artio- and perissodactyls from the Middle Eocene Geiseltal (Germany).
Photos by A. CLAUSING and E. SCHEINER, Martin-Luther-University Halle.

A: Artiodactyl inc. sed., fragment left mandibula ZIN 34493 from Zhylga 2 locality, detail of left P/2, buccal view, magnification 27x.
B - F: Diacodexeid indet., fragment of right humerus ZIN 34492 from Zhylga 1b locality. B - anterior, C- posterior, D - medial-, E - lateral- and F - distal view, magnification 4x.
G: *Anthracobunodon neumarkensis,* fragment of right humerus GMH XVIII 164b from Geiseltal, anterior view, magnification 4x.
H: *Propalaeotherium parvulum,* fragment of right humerus GMH XIV - 1606 from Geiseltal, anterior view, magnification 4x.

3 Discussion

The dentary fragment from the Zhylga 2 locality is provisionally referred to artiodactyls because of the relatively complex P/3 structure with one main cusp and small paraconid and hypoconid. This dentary fragment differs from the mandible of the arctostylopid *Kazachostylops occidentalis*, the previously largest mammal from the Zhylga fauna, by having narrow elongated premolars, remaining P/2 morphology, and a thinner and deeper dentary. The mandible has a sturdy effect due to the low premolar crowns. Compared to Asian species such as *D. pakistanensis,* the premolars of the Kazakhstanian specimen show a higher degree of molarisation. The mandible is more similar to genera like *Diacodexis, Eurodexis* and *Messelobunodon.* Striking is the strong corpus mandibulae in comparison to the small teeth. Nevertheless, artiodactyls are the most probable group, because of bigger dimensions in perissodactyls and the more primitive tooth character in all other orders. In summary, it is not possible to determine the mandible beyond the order level. Therefore, we prefer to use the open nomenclature as Artiodactyla inc. sed.

At specimen ZIN 34492 the reduction of the epicondylus medialis, the crista humeri, the presence of a deep fossa olecrani perforated by a large foramen supratrochlearis, and an anterior groove on the capitulum humeri indicate a cursorial locomotion for this animal. All these features, especially the absence of prominent epicondyles, imply primitive perissodactyls or artiodactyls.

Tab. 1: Comparison of osteometric measurements [in mm] of the humerus fragment from the Zhylga 1b locality (Kazakhstan) to other localities

H Tr - largest height of the trochlea humeri
B Tr - largest breadth of the trochlea humeri
B Cap - largest breadth of the capitulum humeri
B Hum - total breadth of distal humerus joint
(1) data of ROSE (1985: tab. 1,2); (2) data of ROSE (pers. comm.); (3) data of FRANZEN (1981: tab. 4)

Species	Number	H Tr	B Cap	B Tr	B Hum
Diacodexeidae indet.	ZIN 34492	12,0	5,3	15,8	19,3
Diacodexis metsiacus	USGS 2352 (1)				8,2
Messelobunodon schaeferi	SMF ME 510 (3)				ca. 15,0
Bunophorus sp.	UC 30932 (1)				15,5
Wasatchia cf. *dorseyana*	USGS 16470(2)				ca. 20,0
Anthracobunodon neumarkensis	GMH XVIII-164b	8,2	4,2	10,2	13,8
Haplobunodon mülleri	GMH XXII-553	10,0	4,4	11,2	14,7
Anthracobunodon weigelti	GMH XXII-761	9,1	4,2	10,0	14,4
Anthracobunodon weigelti	GMH XXXVII-148	10,7	4,7	11,1	15,2
Propalaeotherium parvulum	GMH XIV-148	13,0	4,3	15,6	18,1
Propalaeotherium parvulum	GMH VII-220	14,9	6,8	18,9	22,3
Propalaeotherium voigti	GMH XXXVII-85	14,3	5,5	19,4	24,7
Propalaeotherium isselanum	GMH XXXVI-128	20,5	6,6	24,7	27,8

Similarities exist to early perissodactyls as *Heptodon, Hyracotherium* and *Propalaeotherium*. The size of the Lower Eocene *Hyracotherium* and the oldest species of *Propalaeotherium, P. parvulum* of the Middle Eocene, is about the same as in ZIN 34492. All mentioned perissodactyls have a supratrochlear foramen. The outline of the humerus is slender because of very weak or absent epicondylus lateralis and medialis. *Propalaeotherium* is different to the described specimen by the lack of a facies articularis radii on the anterio - lateral side of the trochlea humeri. The trochlea ends with the capitulum and has an oblique, but straight lateral border, see plate 1/h. The fossa olecrani is narrower than in ZIN 34492. Other species of *Propalaeotherium* are larger. Higher morphological similarity exists to *Heptodon* and *Hyracotherium*. These genera have a facies articularis radii near the capitulum. In comparison to the Kazakhstanian specimen, it seems that this surface lies more in the depth, near the epicondylus lateralis, see ROSE (1990: fig. 5). ZIN 34492 has this articulation surface in form of little collar in direct connection to the capitulum. The lateral border of the trochlea humeri is plump, see fig. 2/d. Ultimately, further comparisons and more material are necessary to exclude primitive perissodactyls significantly. Its determination as an artiodactyl is more likely because of the described general form of the joint and slender shape of the humerus (GENTRY & HOOKER 1988). ZIN 34492 resembles North American species of *Diacodexis, Wasatchia* and *Bunophorus*. They differ mostly in details, not in the composition of articulation surfaces on the condylus. It differs from *Diacodexis,* represented by *D. metsiacus* (ROSE 1985: fig. 4/1), by a raising of the lateral margin of trochlea humeri into a sharp ridge bordering a groove for the caput radii. In *D. metsiacus* the capitulum humeri is more developed, forming a rounded ridge. The distal breadth (see tab. 1) is smaller than in the present specimen. Therefore, *Diacodexis* is regarded as a small genus relatively specialised by its longer articulation surface for the radius. An exception is *D. pakistanensis,* representing the most primitive artiodactyl up to now. It is by far smaller than the Kazakhstanian specimen and displays graceful articulation surfaces on the humerus, see THEWISSEN (1990: fig. 1/15). *Bunophorus* (UC 30932) and *Wasatchia* (USGS 16470) are comparable in size to ZIN 34492, tab.1. Both are more advanced, as indicated by a medial rim, which is higher than the capitulum. Laterally on the trochlea humeri exists a long articulation surface for the radius. In ZIN 34492 this articulation surface reaches the middle of the trochlea only. Comparing the above mentioned two North American specimens, the nearest morphological connection of the Kazakhstanian humerus exists to *Bunophorus* sp. (UC 30932). The morphological differences from *Bunophorus* and *Wasatchia* are interpreted as a fortification of the articulatio humero-ulnaris: the elbow gets a better stabilisation for a cursorial locomotion. This transformation occurs simultaneously with the reduction of the rotary mobility in the articulatio humero-radialis.

The similar development is to be observed by European artiodactyls of the Middle Eocene. Unfortunately, no older humeri are preserved. Forelimbs are described from *Messelobunodon, Masillabune, Haplobunodon* and *Anthracobunodon.* All these genera are smaller. Postcranial material of *Meniscodon,* which could reach the size of the Kazakhstanian specimen, is not known. *Messelobunodon schaeferi* from MP 11 of Messel, see FRANZEN (1981: pl. 9), seems to have a similar humerus structure as *Bunophorus* and *Wasatchia*. The epicondylus medialis is more developed as in ZIN 34492. Additionally, *M. schaeferi* lacks a foramen supratrochlearis. The second specimen, SMF ME-1001 from Messel, is significantly smaller, see FRANZEN (1983: tab. 5, 6). Although a foramen supratrochlearis exists, the form of the condylus humeri is different. SMF ME-1001, which is referred to diacodexeids according to ERFURT & SUDRE (in press), has a crest-like lateral border. Due to a broad lateral articulation surface for the radius the capitulum humeri seems to be nearly in the middle of the condylus.

Further humerus fragments were found in the lignite deposits of the Geiseltal near Halle. The material, see tab. 1, belongs to MP 12 (untere Mittelkohle: site XVIII) and MP13 (obere Mittelkohle: site XXII, XXXVIII). All specimens are characterised by a foramen supratrochlearis. They have smaller dimensions than ZIN 34492. The trochlea humeri is higher developed by an integration of the capitulum humeri in the trochlea, see fig. 2a, 2c, 2e. Including the specimens from Messel (MP11), *Anthracobunodon neumarkensis* from MP 12 as well as *Haplobunodon mülleri* and *Anthracobunodon weigelti* of MP 13, the following tendency in the development of the distal humerus is evident: the condylus gets a cylinder - like shape diminishing on the lateral side. The epicondylus medialis is developed into a small pyramid - like elevation, giving the insertion surface for the ligamenta collateralis and flexor muscles. This development starts in the Lower Eocene by transforming the capitulum humeri from an independent articulation roll (condition of *Diacodexis pakistanensis*), standing laterally on the condylus humeri, to a small intercondylar ridge. The ridge is dividing the condylus into two grooves. During the Middle Eocene, a further emphasis of the lateral partition of the articulatio humero-radialis takes place (artiodactyles of the Geiseltal). The described specimen from Kazakhstan documents a stage in the development of the elbow, previously not known in Asia: This stage is close to the condition depicted by North American early Wasatchian artiodactyls (*Bunophorus)* or perissodactyls (*Hyracotherium*). Consequently, the Zhylga 1b level can be dated no younger than late Graybullian, (Wa-5 zone, about 53 Ma; CLYDE et al. 1994) that is roughly equivalent to early Ypresian on the European scale.

About this time, due to the great Ypresian warming, the most prominent warming during the whole Cainozoic epoch, the mammalian fauna was remarkably uniform in the Holarctic, as was known previously from the North American and European data. The subtropical conditions prevailed at high latitudes during early Ypresian and provided the most intensive interchange between North America and Europe during the whole Cainozoic (WEBB 1985). The recent discoveries in the Wutu Formation in Shandong Province, China of "pure" North American mammalian groups, such as neoplagiaulacid multituberculates, carpolestid primates, ischyromyid rodents, epoicotheriid palaeanodonts, phenacodontid condylarthrs, together with a new genus of artiodactyls (TONG & WANG

1994, 1995; TONG & DAWSON 1995; BEARD & WANG 1995) showed that this uniformity took place also, at least in some areas, in Asia. In this respect it is noteworthy to point out here, that the mammalian fauna from the Zhylga 1a locality contains at least one predominantly North American group, ischyromyid rodents. There are groups with Holarctic distribution: Arctostylopidae and Nyctitheriidae (NESSOV 1987b; AVERIANOV 1995). Both Zhylga and Wutu faunas were communities, indicating humid circumstances. They existed near the Ocean shore under apparently humid tropical or subtropical climate. By the abundance or predominance of "cosmopolitan" elements, they contrast considerably with the more continental early Eocene mammalian communities. These communities lived under prevailing semi-arid to arid subtropical or tropical conditions and are characterised by the dominance of endemic Asiatic forms. The arrangement of earliest Asian, already highly specialised artiodactyls to these humid communities may indicate that the origination of the order took place in a humid tropical environment in southern Asia. Only later they spread out to the more continental areas with semi-arid to arid climates.

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